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Proceedings of the Ninth Southern Conference on Forest Tree Improvement

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Proceedings of the NINTH

SOUTHERN CONFERENCE ON FOREST TREE IMPROVEMENT

Knoxville, Tennessee June 8-9, 1967

Sponsored Publication No. 28 of the
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Proceedings of the NINTH
SOUTHERN CONFERENCE ON FOREST TREE IMPROVEMENT

Knoxville, Tennessee • June 8–9, 1967

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GENERAL SESSION, JUNE 8

THEME: FOREST TREE IMPROVEMENT—PROGRESS AND OUTLOOK WHERE WE STAND ON PROGRAMS:

Cooperative University and Industry Programs

BRUCE J. ZOBEL [1]

It is not possible to talk about cooperative programs without including the participation of public agencies, which are an integral part of the cooperative effort. The North Carolina State Cooperative includes twenty pulp and paper industries and three state organizations. State agencies also participate in the Florida and Texas cooperative programs. Our supporting industries were eager to have state participation, for improved trees obtained from state nurseries benefit us just as much as improved trees from our own nurseries.

The objective of the cooperative programs is to get as much production from each acre as soon as possible. The urgency is great--at no previous time in history have the pressures for land and timber been so great. Until recently, foresters and industrialists have recked along, quite complacent about the adequacy of the raw material. Published figures showed growth greater than drain, and the main job of many procurement men was to keep too much timber from coming into the woodyards. Several years ago, one person from our own university published an item in a local paper entitled "Let's Plant Trees--but--Who Will Use Them?"

This complacency has been thoroughly shattered. No longer do we hear about the timber surplus. Periodically, the companies in the Southeast find themselves scrambling frantically to keep a supply on the woodyard. Lack of labor, lack of rail transport, and good prices for agricultural products contribute but availability of timber at a reasonable price is a major consideration. Land is more expensive, competition for wood keener, stumpage prices higher, reluctance for the farmer to sell greater. No longer are the great reserves for emergency such as Alabama available. No longer can a company have its land partially productive and buy more land to keep up with mill expansion. High value of forest land and high taxation make it necessary for every acre to produce the maximum. During the past several years, several organizations have been operating nearly full-scale on their timberland areas reserved for emergencies--some are cutting five years ahead of their management plans. Some have satisfied their administrative people by juggling rotation ages so it looks as if their timber supply is adequate. But none of this helps produce more timber.

Here is where tree improvement programs come into the picture. The need is great for both pine and hardwood, but unfortunately we have too little and it comes too late. Seed orchards in our cooperative produced enough seed to plant 20,000 acres this year, only about ten per cent of our needs. If we had started just five years earlier the situation would be much improved. The problem is getting particularly critical for hardwoods.

The cooperatives are booming! We no longer say what gains we hope to achieve; we talk about what we have achieved. We know disease resistance is strongly inherited, there are families nearly completely resistant to fusiform rust and others nearly 100 per cent susceptible. We know straightness of stem and specific gravity of wood can be changed significantly. We have families that produce 300 more pounds of dry wood per cord than others and some where nearly every tree is straight enough to make a pole.

We have one family that has high specific gravity, grows about three cords per acre per year, and produces three tons of dry wood substance per year. In seven and a half years this family grew about four tons more dry wood substance per acre than one of the other selected families under test.

Volume growth improvements have been much greater than anticipated. Fifteen per cent improvement is not unusual and an occasional specific combination has 50 per cent improvement. An open-pollinated progeny test on a poor site, now 15 years old, grew 106 cubic feet per acre per year in check plots while the average yield of the select progenies was 126 cubic feet per acre per year. One family grew 160 cubic feet per acre per year.

There is considerable interest in supplemental sources of fiber from crops such as kenaf or from short-rotation, fast-growing hardwoods. It seems inevitable that these sources will play a part in solving the raw material problems of the industries.

---

[1] Professor of Forest Genetics, School of Forestry, North Carolina State University, Raleigh, North Carolina.

Another source of interest is imported fiber from places such as Brazil or Chile. Growth rates are fantastically high, land costs and labor costs are low. Transportation costs are not too high. As more stability of South American governments is achieved it is nearly certain that members of the cooperatives will draw from these countries more fiber than they are drawing at present. Tree improvement will play a dominant role in such activities.

Nearly every major pulp and paper industry in the Southeast is a member of a cooperative program. They need improved seed, but they also want information and research to help in their management practices. What spacings will be used, what rotation ages followed? Many have studies under way to help in these decisions and in such problems as when to save a log for sawtimber rather than cut it for pulpwood. Nearly every industry is now involved to some degree in fertilization. They need to obtain strains of trees that will respond best and make maximum use of the fertilizers applied. There is a desperate need for strains, hybrids or species of trees that will grow better on poor or marginal sites

The tree improvement cooperative programs, combining the resources of the universities, industries, and public agencies are unique in the world of business. Where else can you find competitors willingly exchanging ideas, plant materials, equipment, and aid? Where else are research findings made immediately available to all concerned? Where else are frequent meetings held at which free exchange of information is given?

In summary, I classify the cooperative industry tree improvement programs as unqualified successes. They have been too late to meet the present acute need, but not too late to make a major contribution. Their secondary effects on forest management and wood utilization have been strong, and forestry in the South feels their influence. Despite all this, they need strengthening.

Research is lagging and more students are needed. Problems such as graft incompatibility, efficient cone harvesting, and proper use of systemic insecticides need attention. Emphasis has been on the more applied phases of forest research, but better liaison must be established with other research organizations. Most importantly, effort needs to be placed on second- and third-cycle breeding for much greater improvement than has been obtained from our current seed orchards. And finally, the supporting organizations have to keep those of us involved in the cooperative programs on the ball. Accomplishments in a short time are good, but the main benefits lie ahead.

State and Federal Programs for Southern Forest Tree Improvement

JOHN C. BARBER[1]

When the first Southern Forest Tree Improvement Conference was held in 1950, state and federal agencies were probably devoting less than 4 professional man-years to tree improvement in the South annually. Then, the only full-time public research project was an effort to breed slash pine at Olustee, Florida, for high gum yield. There were also some Tennessee Valley Authority and Southern Forest Experiment Station studies that required the part-time services of professional people. Things differ today---federal and state agencies now devote more than 35 professional man-years per year to research and action programs. In addition, these agencies cooperate with each other and with universities and industrial organizations to avoid duplication and do as much as possible with available funds.

RESEARCH PROGRAMS

Most of the 13 Southern states have chosen to support the private and federal research programs within their borders rather than initiate extensive programs of their own. One notable exception is the Texas Forest Service which has one of the oldest tree improvement research projects in the South. Since 1951, its efforts have been directed mainly toward developing loblolly pine that has good form, grows rapidly, has high-quality wood, and is resistant to droughts. Much important information has been learned. Because the Texas Forest Service is a part of the Texas A & M University System, however, the work might be regarded as part of a university program.

A staff officer in the Division of Forestry in Virginia now does full-time applied research into problems related to the Commonwealth's tree improvement program.

The Georgia Forest Research Council does not employ scientists directly, but it finances projects at the University of Georgia, contributes substantially to the work of the Southeastern Forest Experiment Station at Macon, cooperates with the Georgia Forestry Commission, and helps to publish and disseminate important research.

Among federal agencies, TVA and the U. S. Forest Service have extensive forest research programs. The TVA program has been under way many years and has accomplished much. Within the last 5 years, TVA has centered its attention on hardwoods. Its research is closely integrated with an action program to provide improved trees for the Tennessee Valley. The program includes selection, breeding, and testing of improved forest trees, and the establishment of seed orchards.

The Southern and Southeastern Forest Experiment Stations are responsible for tree improvement research by the Forest Service in the South. The Southeastern Station's oldest continuing project, that at Olustee, Florida, is now developing fast-growing slash pine with high-quality wood as well as high gum yield. Breeding is now in the third generation. At Macon, Georgia, research by the Southeastern Station was begun in 1954 with the support of the Georgia Forest Research Council in cooperation with Georgia Forestry Commission and the Ida Cason Calloway Foundation. Efforts have been concentrated on loblolly and slash pine. At Athens, Georgia, resistance to littleleaf disease is being studied, and sweetgum and sycamore are being improved. Other important Southeastern Station studies are being conducted at Charleston, South Carolina; Blacksburg, Virginia; Asheville, North Carolina; and Cordele, Georgia.

In the Southern Station, the biggest effort is at the Institute of Forest Genetics in Gulfport, Mississippi. A broad range of problems with both hardwoods and pines is being investigated. The program includes studies of disease resistance, insect resistance, provenance, and the variation and inheritance of many other traits of economic importance in southern timber species. To keep close contacts with theoreticians, one member of the staff of the Institute is in the genetics department of North Carolina State University at Raleigh.

At Stoneville, Mississippi, genetics and breeding studies are underway for cottonwood, sweetgum, and cherrybark oak. Alexandria, Louisiana, is the site of a recently expanded effort to develop longleaf pines that will grow out of the grass stage rapidly; emphasis is on inherent vigor and resistance to brown-spot needle blight. In cooperation with the Georgia-Pacific Corporation, a project at Crossett, Arkansas, is concentrating on loblolly pine tree improvement. Studies of shortleaf pine may begin there soon.

---

[1] Institute of Forest Genetics, Southern Forest Experiment Station, Forest Service, U. S. Department of Agriculture, Gulfport, Mississippi.

In general, the federal programs are providing basic knowledge about the genetics of forest trees. Improved strains of the important species are being developed for all forest owners. Detailed lists of organizations and research efforts in the South were recently published by Dorman.[2]

ACTION PROGRAMS

All Southern States have recognized the importance of supplying high-quality seedlings to forest owners. About 73 percent of the seedlings planted in the area come from State nurseries. Figure 1 shows 1966 nursery production by State; the total is 380 million trees.

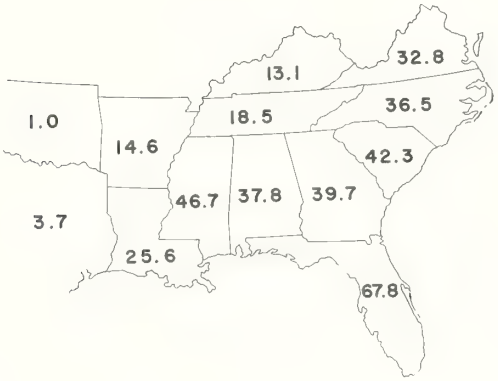

FIGURE 1. Millions of tree seedlings shipped to landowners by State nurseries, 1966. Includes 75% of all seedlings shipped.

To improve the genetic quality of the seedlings raised in nurseries, 12 of the 13 Southern states have established seed orchards. In 10 to 15 years, it is expected that all seeds sown in state nurseries will come from seed orchards. All orchard programs will include some form of progeny testing.

Seed production areas are needed to control genetic quality before the orchards begin producing in quantity, but only a few states have set them up. Kentucky, Louisiana, Texas, and Virginia have a total of 350 acres for loblolly, shortleaf, slash, and white pine seed production. North Carolina is planning to set up an area for Frazer fir. The states with seed production areas and planned and established seed orchards are shown, by species, in Figures 2-5.

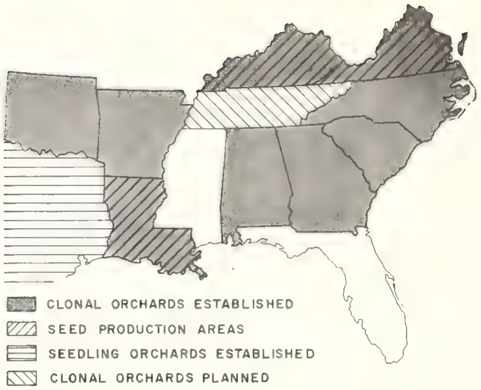

FIGURE 2. State tree improvement programs for loblolly pine.

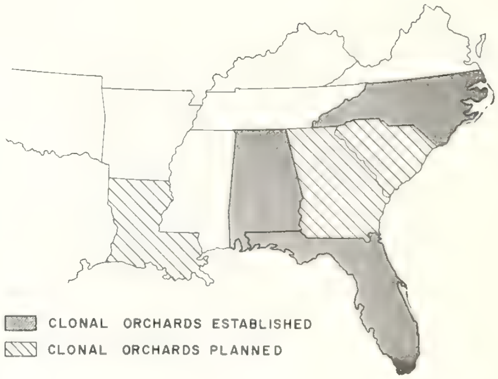

FIGURE 3. State tree improvement programs for longleaf pine.

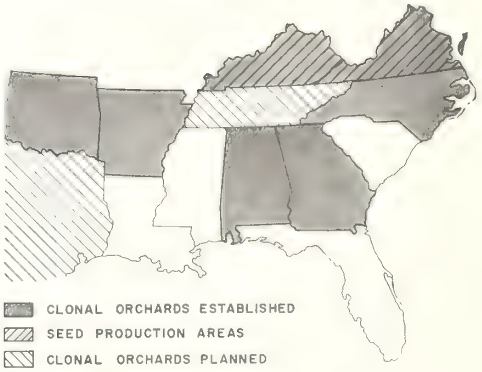

FIGURE 4. State tree improvement programs for shortleaf pine.

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[2] Dorman, K. W., 1966. Forest tree improvement research in the South and Southeast. U. S. Forest Service, Res. Pap. SE-22. 90 pp.

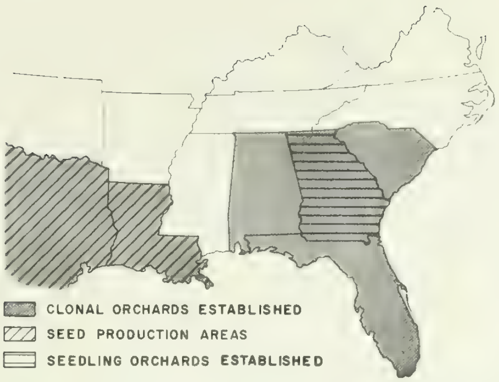

FIGURE 5. State tree improvement programs for slash pine.

When present plans are completed, the States will be operating more than 2,550 acres of pine seed orchards (table 1). They report 1,467 acres now established; about 2/3 is slash pine and 1/4 loblolly. Five other species make up the remainder. As expected, longleaf orchards are furthest from completion among major species. Over half of the 1,084 additional acres planned will be devoted to slash and loblolly, though longleaf, shortleaf, and white pines are strongly represented.

Table 1.--Clonal pine seed orchards in State programs, April 1, 1967

Species	Established	Additional Planned	Total
	Acres	Acres	Acres
Loblolly	346	395	741
Longleaf	31	136	167
Pitch	--	5	5
Pond	--	5	5
Sand	25	45	70
Shortleaf	53	148	201
Slash	948	253	1,201
Virginia	12	18	30
White	52	79	131
Total	1,467	1,084	2,551
State			
Alabama	22	120	142
Arkansas	37	0	37
Florida	576	160	736
Georgia	406	14	420
Kentucky	28	210	238
Louisiana	36	204	240
North Carolina	95	30	125
Oklahoma	13	19	32
South Carolina	95	55	150
Tennessee	0	30	30
Texas	36	7	43
Virginia	123	235	358
Total	1,467	1,084	2,551

Large seedling seed orchards are not planned. Texas has 27 acres of loblolly and Georgia 2 acres of slash pine seedling orchards. North Carolina plans a seedling orchard of Frazer fir, and Texas will expand its loblolly pine orchard.

The development of hardwood seed supplies has lagged far behind that of the pines, primarily because the demand for hardwood seed is small but also because information is needed on the genetics of most hardwoods. The Tennessee Division of Forestry has established 14 acres of yellow-poplar and 6 acres of black walnut clonal orchard for various hardwoods. Several other States are making preliminary plans for hardwood seed production.

TVA has set aside seed production areas for black walnut (20 acres) and white oak (5 acres). Its seed orchards include 82 acres for four species of pine and 39 acres for six species of hardwoods (table 2). Thus, among public agencies TVA and the Tennessee Division of Forestry have all the established hardwood orchards.

TABLE 2--Tennessee Valley Authority clonal seed orchards

Species	Established	Additional Planned	Total
	Acres	Acres	Acres
Loblolly Pine	28	--	28
Shortleaf Pine	29	--	29
Virginia Pine	14	--	14
White Pine	11	--	11
Total Pine	82	--	82
Black cherry	2.8	1.2	4.0
Yellow-poplar	3.3	2.7	6.0
N. red oak	3.0	2.0	5.0
Chestnut oak	1.1	3.9	5.0
White Oak	3.0	2.0	5.0
Black walnut	--	14.0	14.0
Total Hardwood	13.2	25.8	39.0

Region 8 of the U. S. Forest Service is carrying out the largest single program in the country. The program is designed to supply all the seeds required by the southern National Forests, where most pine sites will eventually be planted or seeded for regeneration. A total of 2,557 acres of seed production areas have been established (table 3). In 1966, a poor seed year, about 2,500 pounds of seed were collected from the few areas that had good cone crops. Problems of insect control and cone harvesting are now being studied. These seed production areas will soon be supplying the needs of the National Forests.

The Region is also establishing five clonal pine seed orchards that will cover a total of 1,228 acres (table 4). They will contain 38 species/source combinations. The plus trees have already been selected in all States but Kentucky, which was added to the Region last year, and completion of establishment now depends on grafting success. At the end of 1966, establishment was considered to be 40 percent complete. Seed orchards are planned for several hardwood species.

Another Federal action program worthy of mention is that of the Southeastern Area, State and Private Forestry. This Forest Service organization operates the Eastern Tree Seed Laboratory at Macon, Georgia, and advises on matters of tree improvement from its Atlanta office.

As I hope I have shown in this brief presentation, public programs for tree improvement in the South are well under way. Their early completion, with the limited funds available, depends largely upon cooperation such as that stimulated at this meeting.

TABLE 3--Region 8 pine seed production areas by species and State

State	Loblolly	Longleaf	Shortleaf	Slash	Other	Total
			Acres			
Alabama	36	394	--	10	--	440
Arkansas	10	---	712	--	--	722
Florida	--	266	--	76	--	342
Georgia	10	---	--	--	15	25
Kentucky	--	---	--	--	--	--
Louisiana	35	130	---	85	--	250
Mississippi	--	234	---	80	--	314
North Carolina	34	90	20	--	10	154
South Carolina	60	98	--	--	--	158
Tennessee	5	--	5	--	---	10
Texas	50	15	--	--	--	65
Virginia	--	--	10	--	67	77
Total	240	1,227	747	251	92	2,557

TABLE 4--Acreage in Region 8 seed orchards allocated by species and state

State	Loblolly	Longleaf	Shortleaf	Slash	Other	Total
			Acres			
Alabama	73	30	--	5	--	108
Arkansas	--	--	300	--	--	300
Florida	--	43	--	71	39	153
Georgia	20	--	26	--	28	74
Kentucky	--	--	40	--	--	40
Louisiana	52	14	6	5	--	77
Mississippi	51	34	10	21	--	116
North Carolina	12	12	18	--	29	71
South Carolina	39	35	--	--	--	74
Tennessee	--	--	34	--	43	77
Texas	64	15	39	--	--	118
Virginia	--	--	20	--	--	20
Total	311	183	493	102	139	1,228

WHERE WE STAND ON TECHNIQUES AND SEED ORCHARD CULTURE

Selection of Superior Trees

A. E. SQUILLACE[1]

Most forest tree improvement programs in the south entail some form of mass selection. That is, rather than using random trees as a starting point, tree breeders usually select individual trees that are phenotypically superior in respect to the traits they are interested in improving. Many programs depend heavily upon the benefits of this practice. This subject, therefore, is important to most of us.

I shall not attempt to outline or discuss the various selection techniques employed in the many tree improvement programs of the south. Rather, I shall discuss some of the concepts involved in the effectiveness of mass selection and then make a few suggestions for increasing the efficiency of this practice. The discussion will be limited to selection as it applies to selective breeding programs, with emphasis on southern pines.

The Basis for Mass Selection

In mass selection we attempt to estimate the breeding value of trees--the ability of each tree to produce superior progeny. Judgment in this kind of selection is based entirely on the appearance or performance of the tree itself. The technique differs from "progeny test selection," where the tree is evaluated on the basis of the appearance or performance of its progenies.

Mass selection is effective only to the extent that there is some degree of resemblance between parents and their offspring. In other words, to make genetic gains by this technique there must be a positive offspring-parent regression. The extent of the offspring-parent regression depends greatly upon the magnitude of the environmental effects in the parental population. If such environmental effects are strong, the offspring-parent regression will tend to be weak and genetic gains will tend to be small. If the environmental effects are weak, the parent-offspring regression will tend to be strong and gains will be large.

Because of the dependence upon environmental effects, offspring-parent relationships can vary greatly from one population to the next, even if the genetic variances are equal. For example, take a handful of seed and split it into two parts. With one part, establish a plantation in the normal manner on a prepared site. With the other, establish a simulated natural stand by planting the seeds over a period of several years on a rough site and at a highly variable spacing. When the trees mature, make selections in these two stands and grow their progenies in plantations. Which population should show the greatest offspring-parent relationship? Obviously, it would be the normal plantation. The trees in the simulated wild stand will be highly variable because of the induced environmental effects. The parent trees selected here would appear to be superior but often would not prove to be genetically superior upon progeny testing. Selection in the normal plantation would be much more efficient in capturing genetic gains because of the minimized environmental effects.

Other factors that can affect the offspring-parent relationship are the magnitude of the genetic variance occurring in the population and the mode of inheritance. However, there is not much we can do about these with respect to increasing the effectiveness of selection.

But we can do something about environmental effects. We can, for example, select from plantations whenever possible. Lacking suitable plantations, we can select in areas where site, age, and other environmental factors are relatively uniform. Finally, we can attempt to adjust for environmental effects.

Determining the Effectiveness of Mass Selection

The most reliable way to determine the effectiveness of mass selection is to grow the progenies and determine empirically how much gain is made. However, it is usually necessary to grow the progenies for a number of years before they can be properly evaluated. It is desirable to obtain an estimate of the genetic gains to be expected at the time selections are made. In making such estimates we must be careful to use the proper estimates of heritability. Most authors who publish heritability data cautiously point out that their estimates apply only to the populations they worked with or to similar populations. This is especially important when estimating gains from mass selection.

---

[1] Principal Plant Geneticist, Naval Stores and Timber Production Laboratory, Southeastern Forest Experiment Station, Forest Service, U. S. Department of Agriculture, Olustee, Florida.

Most estimates of heritability reported in the literature were determined from progeny data alone. That is, the estimates were based on the resemblances among trees within families. These families were usually growing under plantation conditions on nicely prepared sites, and the heritability estimates apply to selection under such conditions. They would not apply to selection in a wild population.

If mass selection is practiced in a plantation, heritability estimates obtained from progeny data alone may be applicable. But if selection is practiced in wild stands, the heritability estimates should be based upon offspring-parent regressions. Unfortunately, these are relatively rare in the literature. Usually such estimates, for a given trait, are considerably weaker than estimates made from progeny data alone. A good example is available in data reported by Farmer and Wilcox (1966) for eastern cottonwood (**Populus deltoides** Bartr.). Using offspring data alone, they estimated narrow sense heritabilities of .62 and .40 for wood specific gravity and fibre length, respectively. In contrast, heritabilities based upon offspring-parent regressions were only .18 and .32, respectively. The parents were growing under natural conditions.

As another comparison, Squillace and Bengtson (1961) reported estimates of .31 and .18 to .35 for volume growth in slash pine, based upon progeny data alone. In contrast, Peters and Goddard (1961) reported an estimate of .15, for the same trait and species, based upon offspring-parent regression where the parents were growing in the wild.

The difference in the two kinds of heritability estimates in the above examples may be partly due to the fact that the offspring were considerably younger than the parents in both cases and that, in a sense, two different traits were involved. However, the difference in environmental effects between wild stands and plantations very likely was also a strong factor.

Mass Selection vs Progeny Testing

The relationships between mass selection and progeny testing must be considered. These two facets of tree improvement have the same objectives and are often utilized together.

In progeny testing we are not concerned with the extent of the offspring-parent relationship because the environmental variation affecting the parents is not a factor. Through progeny testing, genetic gains can be made even if the environmental effects in the parental population completely mask the genetic differences.

Because both mass selection and selection on the basis of progeny testing can be effective, the important question becomes: How much relative effort should be spent on these two techniques? To get a precise answer to this question for a specific situation we would need to consider all pertinent statistics available, such as the probable extent of the offspring-parent relationships and the relative costs in time and effort. As a general rule, if the offspring-parent relationship is strong, relatively more emphasis should be placed on mass selection. If it is weak, relatively more emphasis should be placed on progeny testing. More will be said on this point later.

Improving the Efficiency of Selection

Following are some recommendations for improving the efficiency of mass selection and increasing genetic gains generally.

1. *Pick the best stands for making individual tree selections.* The reason for this is that stands of trees may vary genetically, even within relatively small regions, because of genetic isolation, clinal variation, or other factors. The stand itself may be a reflection of ancestry and, hence, also of its progeny. The stands should be within the general region within which we plan to utilize the superior material, unless non-indigenous seed has previously proved superior to local sources. By picking the best stands we might make a genetic gain above that made through selection of individuals within ordinary stands.

2. *Prefer stands that are relatively uniform in respect to age, spacing, and microsite.* The ideal stand would be a plantation established from seed collected from numerous trees growing over the region being dealt with. If selections are made in such stands the offspring-parent relationships are apt to be high. Of course, ideal stands are rare, but I strongly suggest that we establish such plantations for species not yet being improved. Lacking ideal stands, we should pick the most desirable ones available.

3. *Make all possible adjustments for environmental effects.* The University of Florida technique for improving the efficiency of selection for growth rate by adjusting for crown size is an example of a rather refined procedure. However, less refined techniques are also possible. Proper choice of check trees, against which the selection is compared, is important.

4. *Concentrate on relatively few traits.* I don't believe we can produce a perfect tree in all respects from one generation of selection. As the number of traits increases, we reduce the maximum possible selection differential on all traits used. The traits chosen should be those that are apt to give the greatest gain, because of high economic value, high heritability, or other factors. The less important traits should receive attention only to the extent of avoiding negative selection. Such traits can receive more attention when beginning the next

cycle of selection, where the trees will be growing in plantations and where we have already made a gain in the more important traits.

5. *Develop and use selection indices.* Selection indices insure the greatest possible gain when selecting for a combination of traits. This is true, not only because of the statistical manipulations, but also because they eliminate much of the personal bias often encountered in selection. The necessary ingredients for constructing refined indices are heritabilities, phenotypic correlations, genetic correlations and relative economic weights. This information is becoming available.

6. *Weigh the relative merits of progeny testing and mass selection.* Application of both techniques will usually give the most genetic gain. The problem is to determine how much relative effort should be allocated to each technique.

If selections can be made in plantations approaching the ideal mentioned earlier, we can get by with relatively few selections and a minimum amount of progeny testing. In some cases, appreciable genetic gains may even be made without progeny testing, through repeated mass selection.

In contrast, if it is necessary to select in natural stands containing variation in age, spacing, microsite, etc., we should spend relatively more effort on progeny testing. The number of selections should be great enough to permit a heavy roguing of clones that do not prove to be superior on the basis of progeny performance.

Most of our current programs, based as they are on selection in wild stands, fall in the latter category. In many cases, enough selections were made to permit roguing of at least half of the clones after progeny testing, and appreciable gains should be made. However, we should now make preparations to maximize opportunities for further improvement in the next cycle of selection. Plantations should be established, as soon as possible, from progenies of large numbers of selections, preferably those proven to be superior. Organizations working with the same species and in the same region should be encouraged to pool their material. In such plantations additional genetic gains should come easier, even through mass selection alone.

Summary

Control of environmental effects in the stand in which selection is made is the key to effective mass selection. Selection should be made in plantations if the seed source is known to be suitable and if it was established from a mix of seed from many trees. Under such conditions the number of selections can be held to a minimum to reduce the cost of progeny testing. For species in which the initiation of tree improvement work will be delayed, we should establish suitable plantations as rapidly as possible to provide material for effective mass selection.

Lacking suitable plantations, the breeder should 1) select from the best wild stands available, from the standpoint of both superiority and uniformity of environmental factors; 2) adjust for environmental factors to the extent possible; 3) select and progeny test relatively large number of trees to permit heavy roguing after progeny testing; and 4) establish plantations from progenies of large numbers of selections, to be used as a base for the next cycle of selection.

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Development of Grafting and Pollination Methods

RAY E. GODDARD [1]

The development of satisfactory sexual or vegetative propagation methods for a tree species usually involves a certain amount of trial-and-error experimentation. To minimize these empirical tests, two types of knowledge are essential. The first requirement is information concerning the biology of the species which may include anatomy, morphology, phenology, details of normal reproduction, and inherent limitations of the capacity to reproduce by seed or asexual means. Secondly, a thorough familiarity is needed with basic techniques of grafting and pollinating, the tools needed, and the various materials that facilitate the work. Much information on these topics is recorded in forestry and horticultural literature. Thus, the tree breeder or grafter has a large background of useful experience available which can be used to aid the establishment of an efficient program.

Grafting success depends basically upon achievement of a rapid union and prevention of scion desiccation until the union is formed (Neinstaedt, 1961). Most of the union tissue is formed by the stock plant (Mergen, 1954). All of the various methods and special procedures of grafting are directed toward facilitating the union of the two parts and maintaining the viability of the rootless scion until an effective union has formed.

Similarly, controlled pollination involves collection of pollen and maintaining its viability during pollination and the processes that lead to fertilization of the egg. Additionally, controlled pollination implies prevention of pollination from other sources.

Once the basic procedures have been learned, both pollination and grafting require doing the right thing at the right time in the proper amount to achieve success. Pollination, to some extent, and grafting, in large measure, are arts. The traits which make for a proficient practitioner are difficult to define, but close attention to detail is important in both grafting and pollinating. This paper is a review of the relative success in developing propagation methods for the tree improvement programs of the South.

Grafting of Pines

The many hundreds of acres of pine seed orchards now established in the South furnish ample evidence that successful grafting procedures have been developed. Although the largest portion of these orchards are loblolly and slash pines, smaller areas of Virginia, shortleaf, pond, sand, white, and longleaf pine grafts have been planted. Details of methods and grafting techniques employed in this task are almost as numerous as the individual tree improvement programs, or even the individual grafters involved. However, there are only a few general types of operations.

A convenient method of classifying grafting procedures is by site of the grafting operations. By this division, the major methods employed are pot grafting, field grafting, nursery bed grafting and approach grafting. Each procedure has several minor variations and certain advantages and disadvantages.

For pot grafting, year-old nursery seedlings are potted for grafting stock. A major consideration is stock vigor - the stock must form most of the tissue of the union. Potting of bare root stock must be done several months or even a year in advance of grafting so that stock plants may be fully recovered from transplanting stock. Use of long-potted stock plants has caused trouble with windthrow and root girdling. This difficulty can be avoided by use of a transplant tool which moves a ball of soil with the stock plant, greatly reducing the time necessary to hold the plant in the pot. Stock can be grafted one month or less after transplanting. Grafting of potted stock is often done in a greenhouse. At a minimum, a shade house is needed. Its advantages are convenience for the grafter, ease of supervision, some control of adverse climatic conditions and convenience of aftercare of the grafts. However, pot grafting is the most expensive method due to the expense of potting and transportation.

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Approach grafting, which also employs potted stock, has been used on a limited scale. The potted stock is placed adjacent to an established graft (a platform is frequently required) and a branch of the tree is grafted to the seedling stock without severing the connections to the tree until the graft union has developed. The procedure is usually highly successful but is not suited to extensive use because of the expenses involved and physical limitations. Also, the resulting graft is often misshapen as considerable bending is frequently required to match the stock to the scion and the bend is maintained for several weeks while the graft union is developing.

A method especially well adapted to large-scale operations is nursery bed grafting. Stock is grown in beds at low density (a procedure also useful in producing stock for pot grafting). As the name implies, grafting is done directly on plants in the nursery beds. A major advantage is the high vigor of the stock plants. Also, the work is concentrated for an efficient operation during grafting and for the essential after-care. Grafting is usually done in winter or early spring and successful grafts are transplanted to the orchard in mid-summer or fall. At transplanting, the grafts are about two feet tall or larger. Mortality during this phase may be as high as 10% and must be taken into account when planning. In spite of transplanting problems, several agencies with large grafting programs feel that the lowest cost per established graft is obtained by nursery bed grafting.

Field grafting requires no special facilities other than a seed orchard site. Nursery-run seedlings can be planted, two or three to a spot, at the desired spacing in the orchard. Grafting is done a year or two later. With this method, growth is usually superior to that in orchards established in any other manner. The two major disadvantages are relative inefficiency of grafting and after-care and somewhat higher exposure to vagaries of the weather. Individual grafts of a clone are scattered over a large area, requiring moving of materials and equipment a considerable distance between each graft. Late freezes, wind storms and extreme drying conditions can be catastrophic in field grafting.

There are numerous grafting techniques that may be applied. The cleft graft is most commonly used with southern pines whereby the scion stem is formed into a wedge, the top portion of the stock plant is severed, the stock stem is split, and the scion wedge is placed in the split and bound in place.

Side grafting is also frequently employed. This may be a veneer graft in which only one side of the stock and of the scion are cut and the two wound surfaces are bound together, or a wedge scion placed in a split made in the side of the stock plant.

Variations include the whip graft used with or without a tongue to give added strength. A special variation of the veneer graft now seldom used in the South but favored in some locations (Slee, 1967) is the bottle graft in which a tail left on the scion below the cut is placed in water to avoid desiccation prior to formation of a union.

The art of grafting is in the application of grafting techniques. Some grafters develop a special aptitude for making the cuts of proper size and proportion, matching stock and scion tissues, and binding them in place with just the proper firmness and security. The principles of grafting can be taught but real skill is developed only through practice. Some people never develop a real knack for the job.

After the scion is in place, other procedures that affect grafting success or failure are related to protection and care of the plants, pruning of stock limbs, and establishment of the grafts in the orchard. The critical problem for the first several weeks is prevention of desiccation of the scion. This is accomplished by removing a large portion or even all of the scion foliage and by maintaining a humid atmosphere around the scion. Polyethylene bags surrounding the scion and, usually, a portion of the stock plant trap transpiration water and provide an excellent humid atmosphere. In some localities, the bag need not be completely closed and the bag has been omitted with good success in some cases.

Freezing weather can be detrimental. Field grafting in the more northern areas must be delayed until early spring. It is often difficult to schedule operations to avoid late cold snaps.

Considerable heat can develop inside a plastic bag if it is completely closed around the plant. To avoid heat damage, some shading is required. Potted plants can be kept in a shaded location until the polyethylene is removed. In nursery beds and in field grafting, kraft bags are placed over the plastic to provide shade. Where grafting must be done in the spring and there is danger of either hot or cold weather, the graft may be wrapped in aluminum foil before the kraft shade is put on. To protect the grafted plant from insects, dust with malathion or other insecticide before the protective covering is put in place.

For high degree of success, tender loving care of each graft is essential for several weeks. Soil moisture should be maintained at near optimum levels. As the scion shows signs of development, both the kraft and plastic coverings must be removed in two or three stages to avoid sudden changes in conditions. Overly vigorous growth of the stock plant must be cropped back to allow the scion to assume dominance, and any insects that appear on the scene must be promptly controlled.

Potted and nursery bed grafts must be transplanted. If transplanting is done during season of ample rainfall and the plant has not been held overly long in the pot, there is usually little mortality of potted stock during this operation. Moving nursery bed grafts requires more drastic disturbance of the root system and some loss can be expected. Transplanting mortality is minimized if a large transplanting tool is employed which moves a ball of nursery soil with the graft. Such devices have been developed for manual and for machine operation. As with potted grafts, transplanting should be done in the rainy season to aid rapid reestablishment of the damaged root system. Midsummer transplanting operations have been very successful in the lower coastal plains, but fall planting is preferred in areas of low summer rainfall.

A remaining problem which has thus far defied solution is incompatibility of stock and scion. Incompatibility implies the failure to achieve a successful union. Such failure sometimes occurs immediately. In addition, there are forms where the scion portion of a graft gradually fails two or three years after establishment. After poor grafting technique, mistakes in after-care, and unfortunate weather conditions are taken into account, some clones have an inordinantly high failure rate. Little information is available concerning physiological and biochemical phenomena related to grafting woody plants but investigations with herbaceous species indicated increased cytochrome oxidase, polyphenol oxidase and peroxidase activity (Poda-Chikalenko, 1960), increased content of amino acids and proteins prior to formation of a union (Mikhailova, 1957), and a decrease in activity and level shortly after the union was complete. In grapes, scion and stock having complimentary levels of amino acids and sugars were most compatible (Kolesnik, 1963). Metabolic processes, protein synthesis, and growth are accelerated at the graft union. A stable, presumably useful, protein of one plant genotype may be a destructive agent in another. Research is currently underway at the University of Florida to characterize amino acids, enzymes, phenolic substances, and proteins of known compatible and incompatible graft combinations.

Hardwood Grafting

In general, grafting procedures for hardwoods are similar to those used for pine. In addition, some hardwood species may be budded and others root quite readily. Thus, a wide range of procedures and techniques are available for vegetative propagation of hardwood species. The ease of vegatative propagation varies widely, both between and within genera, but McAlpine (1965) stated that most important species have been propagated by one or more methods of grafting or budding. The list includes maples, oaks, ash, cherry, walnut, yellow-poplar, sweetgum, poplar and a number of other species.

As with pines, procedures must be adapted for individual species and for particular situations. With some species, there is a background of experience available. For example, Funk (1966) listed 34 references on walnut grafting, 7 references on budding, 14 references on rootstocks and 9 references on rooting and layering. For other species, forestry agencies are conducting research to determine more successful and efficient procedures. Dorman (1966) indicated that there are current research projects concerned with vegetative propagation of ash, sweetgum, yellow-poplar, sycamore, and oaks.

The dilettante grafter may be satisfied with expensive, inefficient procedures and relatively mild success. One faced with the establishment of a sizable orchard in a year or two must design a program based on reasonable costs and reliable estimates of the number of plants that can be produced. This stage has been realized for most pine species and some hardwoods. Erratic results are still obtained with longleaf and sand pines and with some hardwood species. Further refinement of techniques is needed. However, as improvement programs for other species are developed, in most cases it will be possible to establish clonal orchards if desired.

Controlled Pollination

Pollination procedures for pines are well developed and reasonable success can be achieved with adequate attention to details and timing. There are numerous minor variations in methods and equipment designed for specific program objectives.

Pollen collection, extraction and storage techniques vary, depending upon the objectives of pollination. For detailed genetic studies, great care should be exercised to avoid contamination by other pollen sources. Such measures as collection of catkins before they begin to open and washing them to remove possible contaminating pollen from the catkin surface, extraction and transfer of pollen from one container to another in a pollen free atmosphere may be required. For general progeny testing purposes, such extreme care is not justified as stray pollen grains will not substantially affect the results.

A procedure which insures pure pollen and supplies an ample quantity for most purposes is bagging of pollen clusters with sausage casing well in advance of pollen shed. Ten or more such clusters supply ample pollen for a number of pollinations. In addition, bagged catkins usually shed pollen several days early. At best, collection and extraction of pollen prior to receptivity of female flowers require a very tight schedule, and any procedure which helps create a time gap is desirable.

All tree breeders prefer to use fresh pollen. However, situations frequently occur in which this is not possible. Pollen storage techniques at refrigerator temperatures (35° to 38°F) and below freezing have been developed. In either case, control of moisture content is essential to maintain pollen viability, but very low moisture is more critical with freezer storage. The technique of freeze-drying may provide optimum storage conditions.

If pollen is in short supply, Callaham (1965) has demonstrated that satisfactory results can be obtained with diluted pollen. Dead pollen of the same or different species provided a satisfactory diluent. Dilution to 30 percent live pollen did not reduce the proportion of sound seed.

Pollination procedures for pines require little discussion. The use of synthetic sausage casing for isolation of female flowers has been almost universally adopted. There are many tools for the application of pollen but most consist of a veterinary hypodermic needle, some sort of reservoir for the pollen and a rubber bulb to force pollen through the needle. Many variations of simple and satisfactory devices can be assembled. With a systematic approach and sound planning, a sizable pollination program can be conducted in a pine orchard without an excessive labor force.

Pollination procedures for hardwoods present a much more confusing picture. The diversity of sexual mechanisms among the several species requires that individual techniques and special tools be developed for each species. Other than the broad statement that pollen collection, isolation of female organs and application of pollen are required, few generalities can be drawn concerning hardwood pollination procedures.

To illustrate the variable requirements for controlled pollination, consider black cherry, yellow-poplar and black walnut. Cherry has perfect flowers, individually quite small, borne in a raceme consisting of 15 or more flowers. Flower development is indeterminant with those near the tip more immature than those at the base of the raceme. Each individual flower can produce one seed. Yellow-poplar has a large flower with numerous spirally arranged stamens and pistils. The conelike fruit produced is an aggregate of samaras. In walnut, staminate and pistillate flowers are borne separately. The pistillate flower is quite small and inconspicuous with usually only two or three flowers in a cluster, each capable of producing only one nut. Walnut is normally wind pollinated whereas both cherry and yellow-poplar are insect pollinated. Obviously, quite different techniques are required for controlled pollination of each.

Familiarity with reproductive structures and stages of floral development are essential for a hardwood breeder. Many of the pollination procedures have already been worked out for the hardwood species in which there is most interest. Breeding techniques have been developed for sweetgum (Webb, 1965), yellow-poplar (Taft, 1962), cottonwood (Schreiner, 1959), walnut (Crane et al., 1937) and for other species. Limitation on controlled pollinations of some hardwoods is not related to lack of techniques but is more closely associated with the small return for the labor involved with species that bear seeds singly or in very small clusters.

Pollination is much simpler in seed orchards than on scattered trees in natural stands. Yet, even in orchards, flowers are most frequently located considerably above the height of the average man. Thus, equipment for getting into trees or for supporting the breeder while he works is unavoidable. Several variations of ladders and platforms have been developed, mostly truck or trailer mounted ladders, platforms or combinations of the two. As stated by McConnel (1965), tree climbing has enough risks without helping it along. Safe rigs should be constructed and safety rules should be developed and enforced by each organization involved.

Summary

Procedures for grafting pines are well developed. Efficient programs involving grafting on potted stock, field grafting, or nursery bed grafting can be organized to fit individual species requirements, climatic conditions and other considerations.

Practical pollination procedures for pines are well established and the required supplies are easily available.

Hardwoods present a much more diverse picture than do pines. Vegetative propagation by grafting, budding, layering or rooting cuttings is possible to some extent for all of the more important species.

Pollination procedures are being developed for the important hardwoods. Special procedures are required for each species.

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Field Testing and Data Handling in Forest Genetics Research

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The two subjects I have been assigned to cover in this paper are such that I can only hope to scratch the surface in the time allotted.

I will attempt to present briefly some of the problems associated with field testing and data handling, and hopefully offer a few suggestions which might be used to attack these problems.

Field Testing

In discussing field testing, I am going to take the liberty of assuming that we have a population of trees (usually a single species) about which we desire information concerning the variation present. The information desired may take the form of estimates of genetic and environmental variances and covariances, test of differences among genetic entries, or both. Although the type of information sought can modify the specific experimental design used, there is usually an orderly sequence of steps to be taken in establishing studies to obtain this desired information.

Mating Designs

The first step to be taken is to decide what system of matings will be used to develop relatives for the study. The choice of the mating design will depend on the objectives of the experiment, the resources available, and the flexibility of application to forest trees. A list of several possible designs and remarks concerning them is given in table 1.

If the main objective of the study is to estimate additive and non-additive genetic variances as well as some measure of general and specific combining ability, the two factor mating designs of table 1. should be considered. It should be noted that, although control pollinations are required for the one factor full-sib design in table 1, it is not possible to estimate separately additive and non-additive genetic variances. This design would therefore, have little utility for estimating genetic variances.

Most of the mating designs in table 1 have been used for estimating genetic variances in forest tree populations and some information as to the number of families required for reasonably reliable estimates of genetic variances has been published (Goggans, 1962; Stonecypher, 1966).

The choice of mating design and number of crosses used in a well designed study for selection or progeny testing can differ from that of a study which has the major objective of reliably estimating genetic variances.

This difference comes about for two reasons. *First,* the study properly designed for estimating genetic variances should be concerned with the variances of components of variance while the study for testing or selection should consider the variances of means. *Second,* some of the populations of interest to the tree breeder can be considered fixed as far as the genetic entries are concerned. In other words, there is more interest in being able to compare accurately the performances of a set of genotypes derived from a number of parents than in making a general interpretation of genetic variances estimated from these entries.

Unfortunately little definitive information has been developed on efficiency of various mating designs and number of crosses required for selection or progeny testing in forest trees. With the increasing availability of reliable estimates of genetic and environmental variances from tree populations, it should be possible to determine the efficiencies of these mating designs for selection. Such information is badly needed.

Environmental Designs

Having arrived at what appears to be the best mating design for the objectives of the experiment, the next logical step in establishing the study involves the placing of the genetic entries in the environment where they will be tested. This placement must be carried out in such a way that the genetic information desired is not confounded with

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TABLE I

Some Mating Designs which have been used in Genetic Studies in Forest Trees

MATING DESIGN	GENERAL DESCRIPTION	GENETIC VARIANCES ESTIMABLE	PROGENY TEST INFORMATION
ONE FACTOR:			
Clonal	Vegetative Propagation	Total	Cloning Value
Half-Sib	Open-pollinated seed or polycross seed.	Additive	General combining ability
Full-Sib	Control-pollination of pairs of parents	Additive + non-additive	General and specific combining ability
TWO FACTOR:			
Diallel	Control pollinations in all possible combinations among a group of parents with or without reciprocals or selfs.	Additive and dominance	General and specific combining ability
Design I	Each member of a group of parents is mated to a different group of parents.	do.	do.
Design II	Each of a group of parents used maternally is mated to each of another group used paternally.	do.	do.

the environment and that the degree of reliability of the information is made as high as possible.

The placement of genetic entries into the environment comes under the topic of experimental design which is such a broad field that time limits a detailed discussion in this paper. I will attempt to briefly comment on some design considerations in relation to genetic studies in forest trees.

The choice of the environmental design, like the mating design, will depend upon the objectives of the study, the resources available, and the degree of precision desired. Basic to any valid experimental design are the conditions of randomization and replication which determine to a large degree the precision attained.

If the number of entries is large, which is frequently the case in genetic variance studies, reduction in block size to obtain within block homogeneity should be considered. The reduction in block size can be achieved by reducing plot size or by using an incomplete block design.

Wright and Freeland (1960) concluded that small plots (one to three trees) were statistically the most efficient in uniformity trials of young red pine *(Pinus resinosa)* and yellow-poplar *(Liriodendron tulipifera)*. Detailed development by Conkle (1963), however, showed that single-tree plots were most efficient for four and five year old loblolly *(Pinus taeda)* and slash *(Pinus elliottii)* pines, but multiple-tree plots were equally as efficient as one-tree plots for trees eight, nine and twelve years old. Evans et. *al* (1961) suggest a plot size of 25 trees. The work at Southlands Experiment Forest (Stonecypher, 1966) on estimates of genetic and environmental variances, indicates a plot size of 10 to 15 trees is most efficient for estimating variances.

If a plot size of ten trees is chosen, the number of entries must be relatively small if block size is to be held at a reasonable level. The size of the block, of course, can depend on the homogeneity of the test site, but it has been our experience that block sizes much greater than one-half acre, are too large on most test areas used for studies of forest trees. If block size is held below one-half acre, the number of entries, with the plot size recommended above, is limited to about 31.

It is to be expected that many tree genetic studies will involve many more than 31 entries. This is particularly true in cases where the objective is to reliably estimate genetic variances. An answer to this problem lies in the use of incomplete block designs. Recently, Snyder (1965) has discussed the use of lattice and compact family block designs in forest genetics research. It should be emphasized, however, that incomplete block designs were developed for reliability of comparisons of means and not for estimates of components of variance (Cockerham, 1963). Therefore, if the objective of the study is estimation of components of variance, the complete confounding of entries in sets proposed by Comstock and Robinson (1952) and used for loblolly pine by Stonecypher (1966) can be employed.

Another problem in genetic studies of forest trees arises because of the difficulty of obtaining progenies from all the desired crosses in any one year. In such cases, the forest researcher is often reluctant to postpone field installation until the mating design is completed. In most instances, it has been the practice to place the material planted in any one year in a randomized block design and to include controls or checks in order to compare entries planted in different years. Theoretically such a design is likely to be inferior to a comparable incomplete block design if one exists (Cochran and Cox, 1957). It is doubtful, however, that suitable incomplete block designs can very often be used because of the difficulty in obtaining the crosses necessary for any desired degree of balance.

Number of replications used should depend on the variability to be expected, degree of precision required, available resources and size of the experimental unit (Federer, 1955). Therefore, it is difficult to specify the optimum number of replications which should be used in a particular study.. Our experience has been that a minimum of four replications per test site should be used in most forest genetic studies.

Field Layout.

The term layout refers to actual placement of the genetic entries in the field according to the experimental design chosen.

The importance of care in field layout cannot be overemphasized. Much precision can be gained or lost depending on how the material is placed in the field.

In general, blocks should be compact with as little variation as possible within them, so that differences on the test site will be associated with the blocking procedure.

It is essential to obtain an idea of the variation of the test site in order to be able to ally the blocks with the positional variation which may be present. Use of soil samples, plant indicators, or even planting of a special "test crop" can be used in placing blocks. Much information is often lost by careless blocking.

Testing in Time and Space. Whether the objectives of a genetic study are estimates of variances, test of means, or both, the application of the results obtained can be severely circumscribed unless the possible effects of genotype-location or genotype-year interactions are considered. Use of estimates of genetic variances or tests of differences among genetic entries obtained from single environments and applied to other environments is extremely risky. Such application is valid only in cases where there is an absence of genotype-environment interaction, knowledge usually not available.

Since generalization of results from genetic studies of forest trees is usually desired, studies should be designed to adequately sample a range of environments.

Testing in Special Environments. It is often possible to evaluate certain characteristics more efficiently in special test areas. For example, in order to evaluate relative resistance of pine to fusiform rust *(Cronartium fusiforme)* it is necessary to insure that test material is exposed to the sporidia of the disease and the fungus has a favorable environment for development. Replication of the test material in time under field conditions will sometimes provide such exposure, but one can never be sure. An alternative, which saves time and space is to plant the test material at close spacing in a special test area which is maintained to insure proper exposure.

Evaluations of other characteristics, such as juvenile wood characteristics (Stonecypher et. al, 1964) and drought resistance (van Buijtenen, 1966), can also be made in special test areas.

Use of such special environments for evaluating certain characteristics can be a low-cost and powerful tool for the tree breeder.

DATA HANDLING

Most genetic studies of forest trees are of a size and complexity which require other than hand calculation methods for complete analyses. For example, if five traits are measured, fifteen analyses are required if it is desired to obtain information on the ten possible relationships among the five traits.

I am not going to spend time on a discussion of the advantages of electronic computers as tools in forest genetics research. The advantages should be self evident to researchers dealing with the mass of data generated by forest genetics studies. I would like to emphasize the word "tools" in the sentence above. Suffice it to say, that no matter how sophisticated an analysis one is able to develop through the use of a computer, the strength of the results is dependent on the soundness of principles discussed above, and on the accuracy of the data generated from the studies. Computer people have a very simple phrase for this: *"Garbage in, garbage out."*

Much of the discussion below is directly concerned with the development of data for analyses by an electronic computer system.

Data Collection

A complete discussion of data collection should include comments on measurement techniques, but because of time limitations, this section will deal with the mechanics of data collection. It should be emphasized, as Pearce (1953) points out, that measurements should be taken to provide records that will describe to others what was apparent to the researcher at the time, not merely to provide data for statistical analyses.

Whether the data taken are to be analyzed by computers or by desk calculators, much time can be saved by careful design of data forms. Such a form should include adequate space for complete identification of the material being measured as well as for pertinent remarks by the observer. There is nothing more exasperating to an analyst than trying to perform analyses of data which were crudely recorded on note paper with poor documentation and little regard for natural grouping.

At Southlands, we have found that it is most efficient to group the data on each genetic entry on a separate form. We also record all identification information on the form prior to field measurement, and the forms are sorted according to the route to be taken by the field measurement crew. Such a procedure decreases the number of labeling errors and greatly speeds up field measurements.

Data Origination

Data origination is a specific term related to computers. It is defined as the translation of information from its original form into a machine-sensible form (Sippl, 1966). While this phase of data handling may appear to be outside the area of responsibility of the forest researcher, it is important to realize that one can greatly influence the efficiency and accuracy of this operation by proper attention to form design and use of the latest peripheral input devices, such as optical readers which are becoming more generally available.

All of us are aware of the great technical advances which have been made in the speed and flexibility of the newer generation of computers. Most of these newer computer systems operate in speeds of billionths of a second, and are capable of analyzing masses of data in a few minutes or even seconds. Such speeds are of little consolation to a researcher if it takes days or weeks to develop the data for presentation to the computer.

It has been our experience that the problems associated with data origination present the biggest bottlenecks to efficient computer use. It should be up to us as forest genetics researchers to stay abreast of the rapid developments being made in devices for improving data handling and to use them when feasible.

Data Processing

It has been disturbing to note that there appears to be a growing dissatisfaction on the part of forest genetics researchers with the results obtained from computers. The dissatisfaction has expressed itself in the form of such statements as: "I could have gotten the results faster from hand analyses", or "I didn't get the information I wanted." In most cases, these difficulties have occurred because of a lack of understanding of the computer or an inability to communicate directly with individuals who are familiar with the computer.

Computer scientists are rapidly developing user oriented languages which should largely solve this communications problem in the next several years. However, it is up to us as forest researchers to become familiar with computer techniques and capabilities now. The large-scale, costly studies now installed can only yield their maximum potential results through the use of these powerful computing tools.

SUMMARY

I have attempted to cover in this paper a brief description of the procedures which are usually followed in carrying out forest genetics research. No matter how involved our mating and environmental designs become, or how intricate the analyses of our data, we must not lose sight of the biological implications of our results. The mere reporting of findings is not enough. We must apply these results to the practical goals of the tree breeder. Application of information from well-designed and analyzed genetic studies can lead to an efficient program for producing superior growing stock for our Southern forests. It goes without saying, that this is the goal for all of us attending this meeting.

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OUTLOOK AND NEEDS IN FUTURE WORK

Cost-Return Relationships of Tree Improvement Programs

LAWRENCE S. DAVIS [1]

Widespread and sustained acceptance of tree improvement programs as a forest management activity by the public and the forest industries can only follow demonstrable evidence of economic worth. Your research to date gives convincing evidence of technical possibility and a suggestion of economic feasibility. This paper will briefly explore the principle questions involved in establishing economic worth.

To simplify, this discussion is confined to tree improvement programs for pulpwood and where all costs are embodied in the seed used for regeneration. In this situation, the forest manager is faced with the conventional investment question of whether the discounted additional sale value of harvested wood exceeds or at least equals the seed costs. Stated as a textbook valuation problem, we are concerned with the equation:

$$\frac{(P^*Q^* - PQ)}{(1 - i)^t} - C \geq 0 \quad (A)$$

where P^* is the price per unit of improved wood in year t

Q^* is the quantity of 'improved' wood harvested per acre in year t

P is the price of 'conventional' wood in year t

Q is the quantity of 'conventional' wood harvested in year t

C is the investment cost in 'improved' seed per acre

t is the time required to produce a crop of 'conventional' wood

i is the discount rate appropriate to the decision maker.

The benefits of a tree improvement program are reflected in a combination of ways. Increased photosynthetic efficiency and disease or insect resistance would cause Q^* to be larger than Q. Qualitative improvements in wood fiber yields should cause P^* to be higher than P. Finally, we would expect the time required to grow a given amount of wood to be shorter for the improved stand.

The textbook valuation problem is always given to us with a nice set of values to plug in and obtain solutions, giving the illusory confidence that there really is not much to it. For this problem it just is not empirically possible at present to fill in the equation and find a solution. What I would like to do in this paper is define the equation elements and indicate the sort of information needed from research. To avoid accusation of being a pure theorizer, the cost aspect of tree improvement will be examined first and covers some work we have recently completed (1).

Seed Costs

The investment cost of improved seed is the difference in price between what the forest manager would have to pay for improved seed and what he would have to pay for ordinary seed. To establish this cost, our study started with this viewpoint and basic question: *"what could a privately owned commercial orchard sell seed for, covering all production costs and making a normal profit?"* In a relatively competitive market this would, in the long run, approximate the expected market price for improved seed. A schedule of seed yields over time is the basic expression of orchard output (Figure 1).

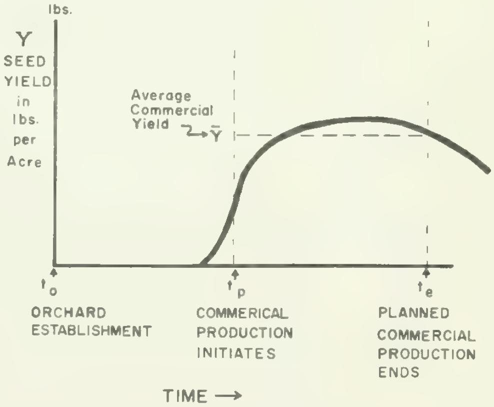

Figure I. Seed Orchard Yield Schedule

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Three major reference points are the time of establishment (t_o), the time commercial production effectively begins (t_p), and the time the orchard is administratively abandoned for commercial production purposes (t_e). Weather and other problems would cause actual seed yields to be variable from year to year but for planning purposes, an average annual seed yield during commercial production, ($\overline{Y}$), is assumed. Associated with this yield and the reference points is a schedule of costs involved in obtaining orchard production. Broken down by major capital outlays, annual operating costs, harvesting costs, and progeny testing costs, the cost schedule is shown in figure 2.

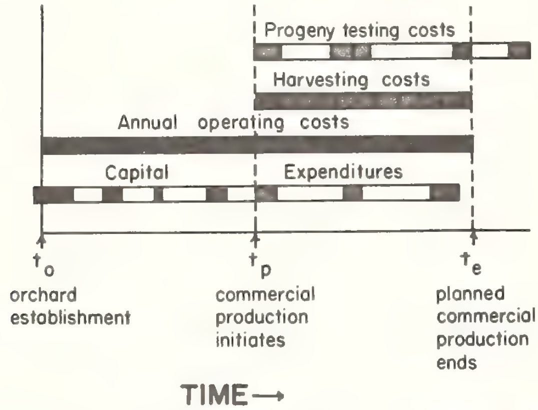

Figure 2. Cost Schedules of a Seed Orchard

To compute a selling cost, the orchard owner is visualized as being at point t_p when commercial production has just started. All establishment costs incurred between (t_o) and (t_p) would be carried forward with interest. The size of a sinking fund required to cover future outlays for progeny testing and capital items can be computed by discounting these anticipated expenses to the present (t_p). The sum of these compounded and discounted costs represents the total value of past and future capital obligations for the orchard at time (t_p) which must be covered by revenue from seed sales. Using a standard amortization formula, the amount that must be recovered each year of commercial production to cover this cost can be calculated. Additionally, the orchard must return enough to cover current operating expenses, harvesting and seed processing costs plus returning the owner a normal profit. A summary equation for these calculations is:

$$\text{SC (seed cost per pound)} = \frac{(k+a)+i\,(a)}{Y}$$

where k is the annual requirement to amortize the capital investment

a is the annual operating and harvesting cost

i is the owners normal rate of return

y is the average annual seed yield expected during commercial production

The right hand expression, i(a), charges a normal profit of i% against current operating costs. This same profit rate is already built into the amortization formula for determining (k). This seed cost, as computed, applies only during the amortization period from t_p to t_e. It is quite probable that the orchard will continue to produce for several years following amortization. However, new research findings and improvements in parent stocks from second generation breeding will likely render any given orchard technologically inefficient and subject to abandonment after a certain period.

Loblolly Pine Clonal Seed Orchard Costs

Data were collected by field visits in 1965 from two loblolly pine seed orchards, a 100 acre orchard in the southeast and a 40 acre orchard in the mid-south. Both orchards were initiated in 1959 and are now nearly complete. The plan of management is well developed for both orchards and future management requirements and cost schedules could be estimated with reasonable certainty. The orchards should be fairly representative of many loblolly orchards since both belong to the Industry-North Carolina State Cooperative Tree Improvement Program whose 19 members all follow approximately the same general plan of orchard management. A listing of management activities found in each orchard is given in table 1. The average per unit management activity costs which are somewhat unique to seed orchards are shown in table 2.

TABLE 1. Planned and observed management activities found on Loblolly pine seed orchards studied

Item	Orchard A	Orchard B
	(amount or frequency)	
1. Plant rootstock	395/acre	195/acre
2. Graft and release rootstock	350/acre	194/acre
3. Mulch rootstock	once	once
4. Fertilize	450 lb. 8-8-8-/acre/year	1000 lb./acre/year
5. Spraying	3 times/year	6 times/year
6. Disking	3 times	once
7. Mowing	3 times/year	5 times/year
8. Site preparation	subsoiling	drainage ditches
9. General supervision	approximately 1/3 of a supervisor and a full time foreman for each orchard	
10. Technical assistance	$25/acre/year	$10/acre/year
11. Clones per orchard	24	45
12. Progeny testing	5-tester system	4-tester system
13. Capital expenditures	integrated with nursery for buildings, equipment and roads	2 buildings, tractor and roads
14. Acres in orchard	40	100
15. Mature orchard density	50 trees/acre	50 trees/acres

TABLE 2. Selected per unit costs for management activities on seed orchards studied.

Item	Cost
1. Planting rootstock	$25 per acre
2. Grafting and graft release	$.75 to $1.50 per graft
3. Progeny testing	
a. one bagged cross	$.13 per cross
b. one acre of progeny outplanted (extra cost)	$20 per acre
c. measurement of outplanted progeny	$100 to $175 per outplanted acre for each measurement occasion
d. present value of total progeny testing costs at the time progeny testing is initiated. (assuming a 5-tester system, a 5% interest rate, and measurements taken at 1, 3, 5, 10, 15, and 30 years.)	$550 per clone tested
e. acres outplanted to test one clone	2 acres per clone (5-tester system)
4. Seed orchard harvesting and extraction costs.	$2.35 per pound of seed
5. Location and selection of parent clones	$150 per clone
6. Estimated total average annual orchard operating expense per acre during commercial production	$217 per acre

Using the previously developed procedure for calculating costs, gross seed costs per pound of seed were calculated for both orchards under a range of assumed interest rates (i), annual seed yields ($\overline{Y}$), depreciation periods (j), and the period before commercial seed production commences (a). Costs were averaged for the two orchards and are shown in table 3.

Based on current information from orchards in the Industry-N.C. State Program and field discussions with several seed orchard managers and research workers, interest rates on the order of 5% and 7%, seed yields on the order of 50 to 75 pounds per acre of orchard, an economic amortization period of from 20 to 30 years and an establishment period of from 10 to 15 years seem to be reasonable estimates in the context of current experience and the viewpoint of seed orchard owners. The circled seed costs in table 3 reflect these estimates and indicate gross seed costs in the range of $7 to $20 per pound. If a single estimate had to be made at this time from the limited empirical base of this study, perhaps $15 per pound would be a reasonable yardstick for seed orchards 'in general'. Such a generalization would be inappropriate and probably misleading if applied to any individual orchard.

Several cost relationships were found which should be of interest to seed orchard investors. First, while cost of seed per pound is fairly low,

Table 3. Average total cost per pound of seed from Loblolly seed orchards studied.

Years before seed production (a) 3/	Average seed yield 1/ per acre in pounds (Y):	30 pounds			50 pounds			75 pounds		
	Depreciation period 2/ in years:	15	20	30	15	20	30	15	20	30
	interest rate (i)	(Dollars)								
10 years	.04	16.85	15.43	12.88	12.21	10.24	8.71	8.21	7.69	6.61
	.05	18.20	16.15	14.16	11.90			8.76		
	.07	21.55	19.40	17.47	13.93			10.13		
	.10	27.37	25.14	23.32	17.45	16.11	15.02	12.49	11.60	10.87
15 years	.04	25.26	23.06	18.50	16.14	14.82	12.44	11.57	10.69	9.11
	.05	26.41	24.64	21.49	18.76			12.66		
	.07	34.65	31.02	27.72	21.79			15.37		
	.10	48.81	44.52	41.06	30.31	27.74	25.66	21.07	19.35	12.97
20 years	.04	30.84	27.73	22.06	19.49	16.44	14.22	13.80	12.56	10.29
	.05	37.73	30.79	26.13	22.42	19.46	16.68	15.77	12.79	11.93
	.07	48.59	42.72	37.52	30.15	26.63	23.51	20.95	18.60	16.52
	.10	77.29	69.79	63.59	47.40	42.90	38.04	36.54	29.46	27.02

1/ Average annual seed yield in pounds per acre of seed orchard during the productive life of the orchard.

2/ Period over which establishment and other costs incurred prior to commercial seed production are depreciated against seed production. Defines the economic or investment life of the seed orchard as a productive asset.

3/ Period between initial establishment of a seed orchard and the initiation of commercial seed production from the orchard.

the capital cost of a seed orchard at the age of initial commercial production is high. For example, assuming a 5% rate of interest, the per acre capital value of the 40 acre orchard at age 15 was $7636 and for the 100 acre orchard it was $4728. Fixed costs of supervision, capital equipment, progeny testing and other overhead expenditures were about the same for each orchard, on the order of $10,000 per orchard per year and amounting to 60+% of total annual costs. Direct variable costs for cultural work ranged from $80 to $120 per acre per year for both orchards. Spreading overhead and fixed costs against a larger acreage resulted in significantly lower annual total cost per acre and cost per pound of seed for the 100 acre orchard. Since observed overhead costs were as low as could reasonably be expected if the orchard were to be properly cared for, establishing the largest orchard consistent with the given supervisory capacity and seed requirements can be recommended as economically efficient and desirable.

As a final observation, the relative cost of parent stock selection is extremely small, on the order of ½ of one percent of seed cost. All of the genetic benefit from clonal seed orchards stems directly from the parent stock selected. From the cost standpoint, relatively lavish expenditures could be made in searching for and testing parent stock without appreciably raising the cost of seed from the orchard.

We haven't considered seedling orchards yet but I assume they would be developed and managed in the same manner as clonal orchards, except for the source of parent stock. If this is the case, then costs per pound should be about the same as from clonal orchards.

Forest Investment Costs of Improved Seed

Reported seed costs (2, 3, 4) for ordinary seed range from $3 to $7 per pound in ready-to-plant form. An average figure might be in the neighborhood of $5 per pound. Subtracted from the gross cost estimate of $15 per pound of seed, a net investment cost of $10 per pound of improved loblolly pine seed is obtained.

A pound of loblolly orchard seed contains an average of 15,000 seeds (5). Ordinary seed is smaller and averages 18,400 per pound (U.S.D.A. 1948). Experience has shown that approximately one plantable seedling per two seeds or approximately 7,500 seedlings can be obtained per pound of improved seed.[1] Using a range of improved seed costs, investment costs per planted acre are shown in table 4.

For normal plantation spacings, from .05 lbs. to .15 lbs. of seed are required per acre. Direct seeding, which uses somewhat more seed, would require a correspondingly higher investment per acre.

TABLE 4. Net investment cost per acre of commercial loblolly pine plantation using improved seed from seed orchards. [1]

Spacing	Number of trees per acre	Net seed cost per pound $6	$10	$16
6 x 6	1210	$.97	$1.61	$2.58
8 x 8	680	$.54	$ .91	$1.45
10 x 10	436	$.35	$ .58	$ .93

Returns to Improved Seed Investments

Manipulation of tree genotypes through either the seedling or clonal orchard route is directed to increasing the quantity or quality of wood yields from commercial forests under a given environment and management regime. I am not sure whether quantity or quality has received the most emphasis in your improvement programs . . . . probably a combination of both. Quantitative improvements are certainly the easiest to evaluate. In equation (A) we simply set the prices equal and determine the increase in rotation value yield due to more wood being present. Not yet knowing the magnitude of yield increases, we can make some management assumptions and, using our estimated seed costs, calculate what the quantity gains must be to justify the seed investment.

Assuming an interest rate of 5%, a constant stumpage price of $5 per cord, and a rotation age of 30 years, the extra yield in cords of wood at rotation age required to justify the net investment costs given in table 4 are shown in table 5.

Again running the risk of generalization, an 8 x 8 spacing and a net investment cost of $10 per pound of seed appears reasonable for current conditions in the South. This would indicate a yield gain of slightly less than one cord at rotation age is required to justify the investment in improved seed. Yields of managed loblolly pine plantations run from 25 to 40 cords per acre at age 30. The needed gain would therefore be on the order of a 2½% to 4% increase over current yields. Published expectations of growth and yield increases summarized by Barber (6) run from 5 to 10% and more based on initial measurements of progeny from clonal orchard parents.

Recognizing the many assumptions used in reaching the cost and required yield increases given above, it is still fairly clear that the investment costs in seed from commercial loblolly pine seed orchards is sufficiently low that realizing only a minimum expectation of increased yield will

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[1] These costs were calculated assuming a pound of either improved or ordinary seed yield 7500 plantable seedlings. While the improved seed have fewer seed per pound, they also are larger and have higher percent viability. If both seed sources had the same ratio of seedlings/seed, the tabled costs should be approximately 9 percent higher.

TABLE 5. Increase in yield cords per acre from 30 year loblolly pine pulpwood plantations required to justify investment in improved seed.

Spacing	Number of Trees per acre	Net seed cost per pound $6	$10	$16
6 x 6	1210	.84 1/	1.39	2.23
8 x 8	680	.47	.78	1.25
10 x 10	436	.25	.50	.80

1/ Assuming: stumpage price = $5/cord, r = 5%

justify them. In short, from the stumpage grower's point of view it certainly appears that current investments in loblolly seed orchards are well within the "ballpark" with respect to financial justification. If the upper expectations of quantitative gains materialize, they should prove to be excellent investments.

Wood Quality Improvements

The last and most intriguing topic covered here is the question of returns due to wood quality improvements. Returning once more to equation (A), we need to know the price or value differential between ordinary wood and improved wood. To my knowledge price differentials do not currently exist and to estimate what they might be, we must travel from the woods and take on the viewpoint of the mill manager.

Wood is an industrial raw material and therefore, quality of this material must be defined with respect to the products and processes in which it is used; in this case, paper making. Given the nature of pulp and paper manufacture, the pulpwood woodpile standing ready to be run into the debarker could be appropriately described as a pile of unseparated cellulose fibers. The relevant attributes describing the raw material might be fiber length (X_1), fiber diameter (X_2), strength (X_3), fiber/lignin ratio (X_4) and so forth. If we could take the woodpile apart and plot the distribution of all fibers by these parameters, we would surely get a well defined distribution (figure 3). In the manufacturing process, the amount of raw material required per unit of product, and the time and cost required to convert the wood into paper, is technically related to these parameters of the woodpile. Pulpwood quality, therefore, could logically be defined as the mean $\bar{X}_i$ and variance $6^2_{X_i}$ of these parameter distributions.

Using this definition of wood quality, changes in quality could occur by increasing or decreasing the mean or variance of these parameters. The value of these changes could be either positive or negative depending on the type of paper or fiber product for which the woodpile is used.

Two empirical questions arise in order to appraise the feasibility of changing any of these parameter distributions in the mill woodpile.

1. *How can the distributions be changed and what is the cost of the changes?*
2. *What is the value of different kinds of changes in the context of a specific mill and product situation?*

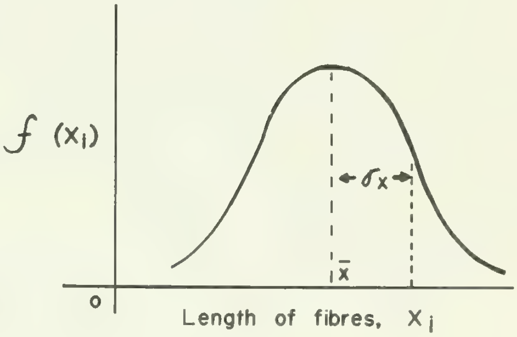


Figure 3. Fibre Length Distribution of Pulpwood in a Mill Inventory

Changes in wood quality

Several possibilities exist for controlling wood quality of which genetic or biological control is but one. Figure 4 illustrates the raw material supply system from woods to millyard. At each stage of the system the general types of quality control activities which might be undertaken are indicated. Procurement and millyard sorting could have at least as great an effect on the parameter distribution or quality of the final woodpile as genetic control in the forest. At the moment I have no idea as to the potential magnitude or costs of quality control made throughout this system. The data presented earlier on seed orchard costs gives some indication of genetic control cost but as yet it hasn't been closely related to the amount of change it can produce in the woodpile.

Research could probably go a long way towards providing some answers to this question. An operations research approach using existing data to simulate parameter distributions and the changes that would likely occur under a variety of control activities could probably be accomplished. Costs of most control activities could be estimated.

Value of Wood quality changes

Even assuming we could get some idea about how to change wood quality and what it costs, we are still faced with the difficult question of determining what these changes are worth. The value of any industrial raw material is derived from the value of the product for which it is used and the

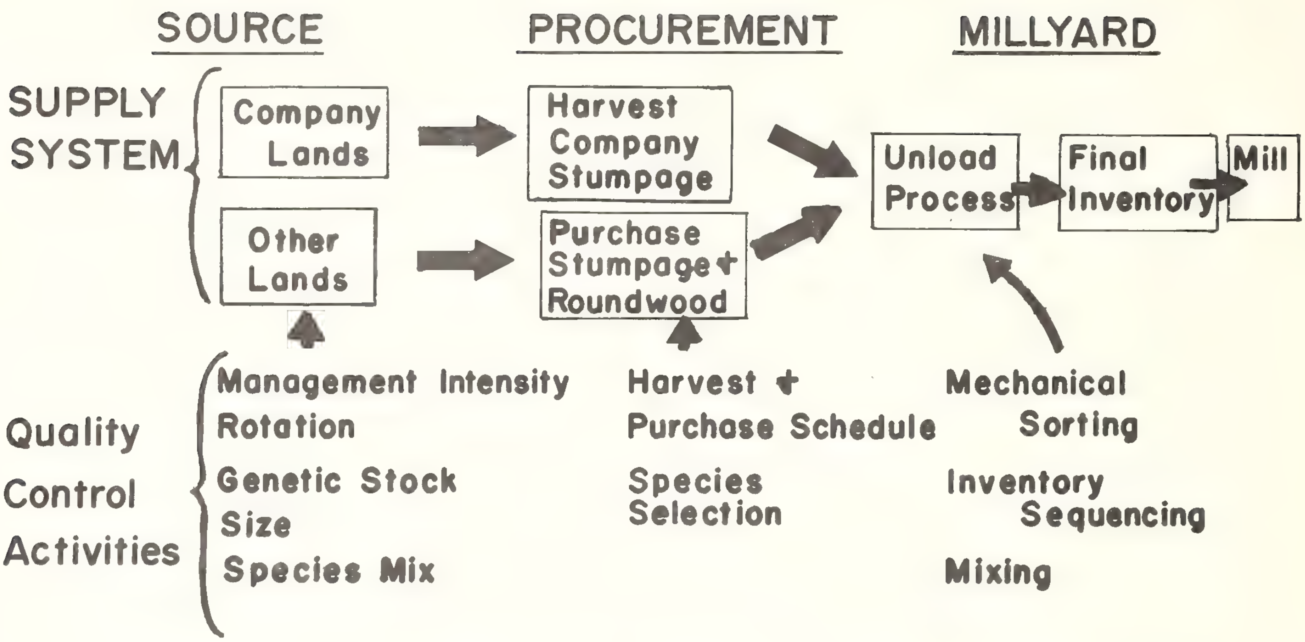


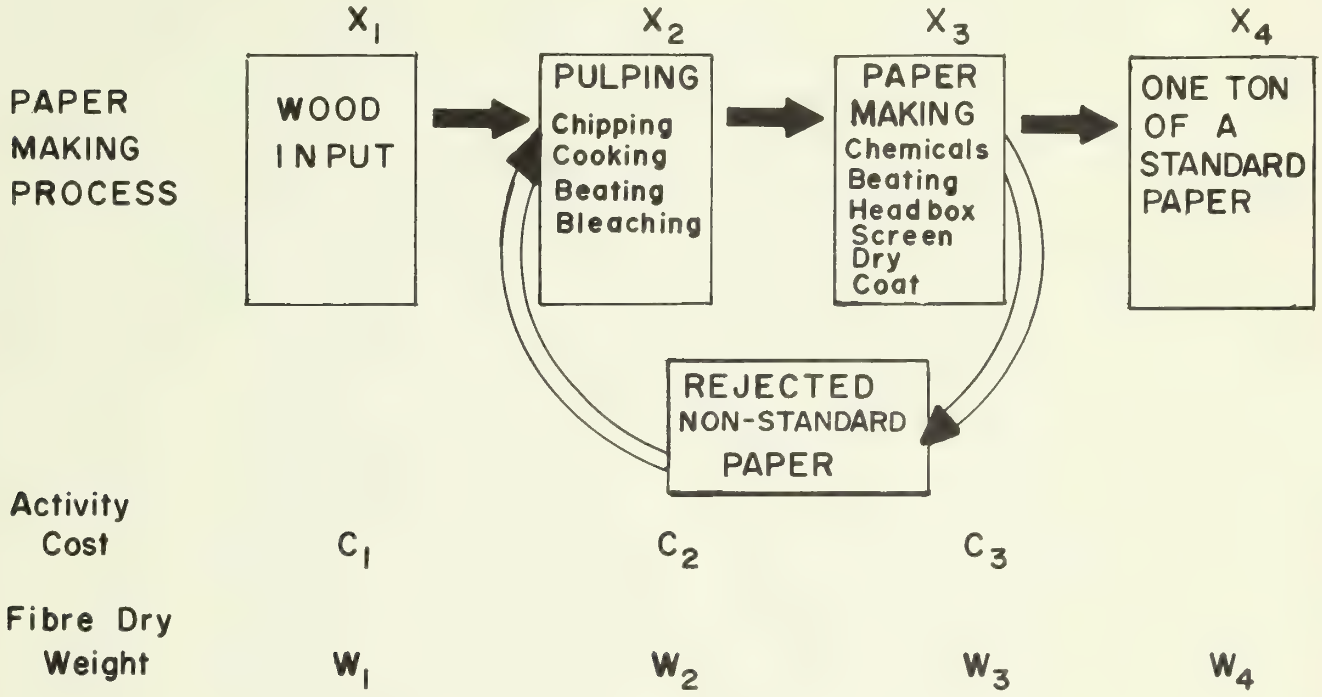
Figure 4. Location of Possible Quality Control in a Raw Material Supply System for a Pulpmill

cost of converting it into the product. To determine the value of controlling quality of the wood raw material, we must accordingly look at the paper making process. Paper making is represented in figure 5. Three main activities are involved; the wood input, pulping, and the paper machine. Each activity has several sub-processes which control the conversion of the wood to the final product. The total cost of a ton of standard paper is the cost of wood (C_1) the cost of pulping (C_2) and the cost of paper maker (C_3).Allowing for some profit, the price of this ton of paper is approximately equal to the sum of these costs.

Within this wood-to-paper conversion process, increases in value and thus price for the wood input would arise if changes in the quality of wood reduce the total cost of producing paper. Control of wood quality could conceivably reduce conversion costs in the following ways:

1. Pulping and paper machine costs (C_2 and C_3) could be reduced. The hypothesis here is that C_2, $C_3 = F(X_1)$ i.e., cooking time and beating requirements might be reduced if the wood were more homogeneous.
2. Reduced wood variability within a given pulping and paper making setup might reduce the amount of finished paper rejected for not reaching product standards. This, at a minimum, would reduce the average pulping and paper making costs by reducing the amount of material that is run through twice.
3. By reducing the dry weight of fiber material needed to produce a given amount of standard paper. To illustrate: suppose if the fiber mix were perfectly controlled, a quantity of fiber W' would be required to construct a square yard of paper meeting certain performance standards of strength, etc. In practice, quality variations are experienced in the manufacturing process and to avoid excess rejections, a larger amount of fiber is used (W'') and the paper is made, on the average, to exceed the specifications. The difference (W'' - W') represents the amount of overbuilding in terms of the wood fiber used. Wood quality control should be able to reduce the difference and result in a cost reduction by requiring less input per unit of output and by reducing average processing costs per unit of output.

My reason for believing control of the wood input could achieve some significant cost reduction is an awareness of the tremendous variation and lack of control found in current mill pulpwood inventories. Pulpsticks vary by age, species, genotype, growth pattern, position of the tree, etc. It is difficult to imagine that reduction in this variability would not have an effect on the conversion process. Given current prices of wood pulp and paper, only a small reduction in average processing costs could result in million-dollar level savings when one considers the volume of raw material passing through a paper mill per year. To determine these potential cost reductions is a difficult research task.



$$\text{TOTAL COST} = C_1 + C_2 + C_3$$

$$C_2, C_3 = f(X_1)$$

Fig. 5 Quality Control and Costs in the Paper Making Process

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Need for Total-Tree Concept

Keith W. Dorman [1]

After listening to a series of summaries as to where we stand on various phases of the Southwide program, it seems any man would be very ungrateful to talk about needs. But we can't stop now. The job isn't done for the pine seed orchard program. It has hardly started for hardwood species and minor pine species.

We have finally entered an age of tree breeding in Southern forestry. The huge pine seed orchard programs are one of the few truly huge and regional Southwide programs in modern times.

The job of producing tree seedlings of improved strains is a big one. It will take time, but it can be done. Other large jobs have been done; you developed a planting program that is bringing thousands of acres into production. You are well underway on fire protection. If you don't believe this, just examine the old photographs taken in Florida woodlands by naval stores researchers in the 1920's. The background scenes are pretty grim. You built a great Southern pulp and paper industry. You not only built it, but you did it in such a way that there are more forest lands and trees now than when you started.

There is a need in our Southwide program for continuing emphasis on creative tree breeding. This will bring into production the improved strains we need. We don't want to lose sight of our main goal amid strong and productive research on techniques and principles. This is not to say we need less research on methods, but rather to say we need more on creative aspects. As interesting as it is, methods research is not the end point of creative breeding. We have to create the trees--whole trees, the total tree--not just traits. Just last month in Washington, the Chief of the U. S. Forest Service told the Forest Industries Committee on Timber Valuation and Taxation that new projections of demands indicate that we will have to *double* the pulpwood cut between now and 1985 to keep pace with expanding markets. This is about 18 years from now. Eighteen years ago we were about ready to organize the Committee on Southern Forest Tree Improvement. A lot of trees are going to be grown in the immediate future.

We want our Southwide program to be known not only for the excellence of its various parts but for the excellent creativeness and productivity of the program as a whole.

We need to maintain the integrity of the regional program. This gathering in Knoxville today and tomorrow is a conference on forest tree improvement. The group sponsoring it is the Committee on Southern Forest Tree Improvement. We meet to discuss improving forest trees, not just forest genetics, not just promising leads, not just improved techniques, but the sum total of all our efforts, improved trees, the total tree.

Before mentioning some of our needs in the future, we might comment on some of the accomplishments of the past. One thing that stands out in a review of accomplishments since 1953 is the contribution of industry to the research and action program. The list of cooperators in research is like a roll call of forest industry. The number of forest industries represented at conferences like this one is equally impressive.

This is a particularly good time to take a brief accounting of where our program has taken us over recent years, and to take a quick look at some jobs ahead. The Committee on Southern Forest Tree Improvement has sponsored a survey of forest genetics and forest tree improvement research in the South and Southeast. Although a report of this kind is out of date almost before it is completed, the 90-page booklet does give a pretty good picture of research. Copies are available at the Southeastern and Southern Forest Experiment Stations.

Another report important in evaluating progress is an extensive summary of the genetics of southern pine species, both major and minor. I've nearly completed the first draft of this paper, and after abstracting over 900 papers that contained research results, I can assure you that there may be things Southern researchers haven't done, but failure to publish articles certainly is not one of them.

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Southern research has made important progress in all broad fields of tree improvement. We tested many foreign species, particularly softwoods. In general, this method of getting improved strains isn't very promising, although it may be a factor locally. Racial variation studies with pines have been numerous and productive, but it looks like the movement of seed long distances is not feasible in coastal regions. In certain local areas inland, it may be more promising. Racial selection studies have pointed out forcefully how great losses in growth could be from using the wrong race of seed. Species hybridization has been carried out at a few locations and there seem good opportunities for considerable genetic gain by combining the best traits of the best individual trees of the best races of the best species for specific localities. Selection within species has received the lion's share of attention, and the estimates of gains possible seem to be increasing rather than diminishing. This gives added impetus to the seed orchard programs. Also, it points out opportunities for substantial improvement through really intensive breeding programs with readily available local trees. This approach to creative tree breeding has great opportunities for the future.

School Problems

There is a need for continuing the strong emphasis on creative tree breeding in teaching and research at educational institutions. Our Southern schools should give great attention to this field of study, as well as to the field of forest genetics. Regardless of which agency or group does applied tree breeding--the Federal government, State forestry agencies, private industry--the men doing it should be well trained. They won't be if the schools don't train them, and the schools won't give them this training unless first-class men are available as teachers or instructors. Present teachers have to teach future teachers who can in turn teach students.

Without good academic training facilities, recognition of the importance of tree breeding, and good job opportunities, creative tree breeding activities will not attract the best minds and the best men. This means that the final step in all forest tree breeding work--that step between research and practice, or between the printed word and the living tree--will have to be taken by the next best, the poorly prepared or the poorly trained.

Tree breeders aren't made in a day. They must be well trained in genetics, and in addition they must know the important factors in utilization of the crop and the culture of the plants with which they work. The necessity for being highly trained or well informed in three broad subject-matter fields is the main reason that creative tree breeding is more complex than is forest genetics alone.

Speaking of plant breeding in general, Professor Caldwell of Purdue University described the problem as follows to the International Crop Improvement Association at one of their annual meetings.

> *"Agricultural development is inherently the ultimate objective of our agricultural institutions. It must not become the neglected stepchild of these institutions. Work on development must be staffed with first-class, creative talent, no less than research work, unless we are to have second-rate work in development. Development work is often much more costly than the research from which it arises, both in industry and in agriculture. While agriculture must, and does, support the great new expansion in basic research, it is beyond comprehension that it would tolerate a simultaneous neglect of the development work that would translate the new research findings into agricultural achievement."*

Trained tree breeders and forest geneticists continue to be in short supply. There is a job here for everyone to increase enrollment in these fields of work.

Southern schools have been doing an admirable job of coordinating but still keeping some degree of distinction between three quite large but different fields of work: teaching, research, and large-scale applied breeding. This is truly a great accomplishment achieved in a short time, and Southern forest industry will benefit greatly.

Silvicultural Problems

Industry can help the overall Southwide program by devising methods of getting strains into use. It takes 10 or more years of breeding and testing to get certain strains of annual crops into production. A schedule of this length is nearly impossible with trees and we should admit it. At the same time, the tree breeder can't ask others to take great chances on his products. There must be a middle ground somewhere. Perhaps the possibility of using mixtures of wild stock and improved strains or mixtures of different improved strains should be investigated. If certain trees do not keep pace with the group they will fall out. They will do this regardless of their origin. Pure plantations are easy to handle silviculturally, but perhaps there are advantages in other types of planting. We have changed our ideas about spacing, intermediate cuts, and rotation lengths, so perhaps we can do it in regard to mixtures. There are various ways of mixing strains. Also, mixtures could be varied from year to year in proportions according to performances of strains planted at earlier periods.

Industry can emphasize creative breeding. We can have scholarships, awards, and other types of recognitions similar to those given now for research. Because of the high values involved, industry publicity men should have a field day with this subject. We have been getting good mileage out of some of the seed orchard programs.

Creative breeding is too important to be left to chance. It requires too many operations, too many jobs in sequence to happen spontaneously. Therefore, we have to make special efforts to achieve it. Industry can support the efforts to bring it about. This they have done and are doing, but we don't want the effort to slacken pace. They should keep the pressure on researchers and educators.

There are strong forces supporting research in methods. Prestige, recognition by colleagues, and good salaries are strong incentives. This is good. The spirit of publish or perish that is abroad in the land puts great pressure on researchers. The best way to obtain something to publish is to make a study. But studies don't mean new trees or total trees, so something in addition is needed. There is a difference between a bad thing and misuse of a good thing. Research is not bad, but unless considerable effort is expended in creative breeding we are being unrealistic about a proper division of our total effort.

Research Problems

In our broad Southwide research program, the process of creating strains and getting them into production should be under constant examination to see where there may be opportunities for speeding up the job. For example, our progeny testing methods for seed orchard clones are expensive, time consuming, and lengthy. If we could demonstrate there was a high correlation between the performance of the grafted trees and their sexual progeny a great savings would be realized because we wouldn't have to conduct progeny tests to verify performance. Perhaps we'll find the correlation may be high for certain traits but not for others. Even so, this may be very important because the traits we do have to test for may be those that require only a few progeny or a few years' time.

Research is generally investigative, whereas tree breeding is creative. One is not a substitute for the other. There has to be a conscious effort to keep in mind the problems and goals of tree breeders and take advantage of every opportunity to move ahead. This helps in choice of research problems and interpretation of results. In other words we have to be tree breeding conscious to make progress. The man who saw a giraffe for the first time and then commented authoritatively that there ain't no such animal was not a trained animal or plant breeder. We have done little better in tree breeding until recently. We looked at fast-growing, well-formed, disease-free trees and said it can't be true. We have said this thing we see can't be genetic so it must be environmental. It was not until we questioned whether or not the effects were environmentally caused that we found out that the trees were correct and we foresters weren't.

It seems that creative tree breeding is becoming one vast problem of sampling, comparing, correlating, and predicting. These are also fields in which statistical methods are particularly useful. We should utilize them fully, not only in research studies but also in creative breeding. Relationships are important, but absolute values are often of greater importance to the tree breeder. In the report of a large study of geographic variation, a discussion of relationships covers 67 pages. The paper contained 68 pages and on page 68 are given the absolute values for the traits studied. There is constant need to scrutinize our study designs to make them produce the biological information we need in the shortest possible period of time. We have many data now on which to work in improving techniques.

In any broad field of biology there is always a need for work on fundamentals and principles. Tree breeding and forest genetics are not exceptions. However, there are some differences of opinion among researchers as to what constitutes good work in these fields.

We should not be misled into thinking that research in fundamental principles is characterized only by the fact that the results may not be useful. Other standards are more important. For one, great imagination must be demonstrated in defining the problem and in developing a solution. For another, the possible results must show great promise for yielding information on principles or procedures that will have far-reaching effects. And last, highly complicated instruments must often be developed and used.

The second characteristic of good research, that it show great promise, is very important. One research administrator has remarked that great imagination should be used to develop a problem and a method for solution, but that when the researcher comes to the justification section of his study plan or project proposal, he should face up to the cold, hard facts of life and ask himself just how important the work really is. Does it really have great promise of contributing to our knowledge of broad and useful principles. If it doesn't, probably the study isn't very fundamental.

There is a great need, I think, to mount a massive attack on the genetics of tree growth rate. In spite of all that has been said and written about breeding fast-growing strains of trees, we really haven't charged headlong into the problem. What are the fundamentals of variation and inheritance of growth? What are the ways in which breeders can influence or increase growth? Will we know more about these factors 20 years from now than at present? Growth is certainly not an easy subject to investigate, but this doesn't decrease its importance. Good estimates of growth performance require extensive replications in time and space. Both of these are very hard things to come by in this speed-up age. But growth studies are so important we will have to make them.

It has always seemed to me that plant physiologists and geneticists should work very closely together. Both work at the very origin of life processes and a combination of their skills should create wonders in creative breeding.

We should not be misled into thinking that if we understand the general principle of how plants work we can manipulate the processes at will. Something more is required. We have to know at what key points we can influence the process by the means at hand. James Bonner, in an article entitled "The Upper Limit of Crop Yield," used this approach. He said, "We have seen that plant efficiencies are in general limited, under high light intensities, by the CO_2 concentration of air. Might it be possible to breed plants for leaves in which there would be increased conductivity of CO_2, in order to lessen diffusion resistance to CO_2 or to shorten diffusion paths?" After describing the limitations of chloroplasts, he suggested that their structure might be altered. He said, "Such a modulating chloroplast should be able to operate at an efficiency equal to the quantum efficiency of photosynthesis over all light intensities from zero to that of full sunlight. Might it not be possible to breed plants for such an improved and more sophisticated type of chloroplast structure? It seems today a difficult problem. Perhaps it is an insoluble one. But it is certainly a goal worth consideration. The fruits would be large indeed." It seems to me that here is a fundamental problem of sufficient importance and complexity to attract the best research minds in the South.

A good research program has a balance between studies in which yields are low but certain and those in which yields may be high but uncertain. Increasing photosynthetic efficiency through breeding might fall in the latter group.

We need all the information we can get on heritability of traits in the classic sense. But, we need to know about inheritance of individual traits in the tree as a whole. As geneticists have pointed out, the environmental component in heritability estimates is of great importance. However, when we review all environmental factors over the southern pine region geographically and the time period required for a rotation, the job of testing all these environmental factors becomes nearly impossible. Creating new kinds or strains of trees contributes greatly to our knowledge of inheritance of specific traits and combinations of traits. Thus, there is a strong research flavor to field studies involving growth of trees resulting from crossing for specific purposes. So, in regard to the question of which should come first, research or applied breeding, it is impossible to tell the cart from the horse.

We are approaching the time in our Southwide program when we should consider progress and problems in terms of species. In genetics research, the subject investigated often is of prime importance. The species used and the geographic location of samples are secondary. We accumulate a large body of information on a subject, but with widely varying species and at different geographic locations. The tree breeder, on the other hand, has to work with a wide variety of subjects but with only one or a few species and at one geographic location. In other words, he doesn't breed trees in general over a wide area, he is faced with a species and its particular problems at a geographic point. Perhaps sometime we should consider holding workshops on breeding for each major tree species. This would help focus attention on progress and problems with the tree right on the ground where the problems occur and work is in progress.

The other day I was reading an account of how the dwarf, high-yielding strains of wheat were developed by plant breeders at Washington State University. The research that has been done and the information accumulated about wheat is so large that it is almost impossible to visualize. Yet, when the particular crop-breeding problem came up with the dwarf types, a lot of work had to be on a trial-and-error basis, using educated guesses by experienced plant breeders. Even then it required nearly 10 generations to develop and test the new strain. The point here is that creative plant breeding can hardly be reduced to a rule-of-thumb process. There has to be consistent effort applied along several different lines in the hope that some one of them will produce the desired result. We shouldn't wait to start breeding until we think we may have all the answers. This may never be, as breeders, working with plants or animals which are much easier to work with than trees, are finding out. Science can contribute greatly, but art is still a requirement in creative breeding.

Conclusion

These are only a few of the problems of importance to the Southwide program, but I think they are major ones. Furthermore, work has been done on all of these and this is good. The greatest need is to broaden current efforts and make them more meaningful. Our Southwide program is very broad. Constant effort is required to keep it under review, and stress the more important of many important problems that apply specifically to the creative breeding work.

New Trends in Breeding Trees for Disease and Insect Resistance

HENRY D. GERHOLD[1]

For many generations silviculturists have been using various means at their disposal to reduce damage caused by diseases and insects to forest trees. The production and use of more resistant varieties is a relatively new way of reaching this objective. Most tree breeding programs that are aiming for improved resistance are still in their infancy. My purpose in this brief review is to point out some examples of recent developments in resistance breeding in order to illustrate the type of work that is underway. Several more comprehensive or specialized reviews are listed after the literature citations.

Sources of Resistance

Opportunities for discovering heritable sources of resistance that can be utilized for tree improvement have increased tremendously in recent years. The ever growing number of provenance and progeny test plantings provides many situations where the latent genetic diversity in resistance may be uncovered and measured after suitable exposure to an insect or pathogen. Accumulating evidence about fusiform rust resistance illustrates this trend. Reports by Wells and Wakeley (1966) and by Wells (1966) enlarge on earlier information, pointing toward geographic regions where selection for resistance should be most rewarding. Studies at North Carolina State (1966) indicate the usefulness of progeny tests for detecting fusiform rust resistance; "... it now appears that perhaps the greatest immediate gain from the Cooperative Tree Improvement Program may be in disease resistance."

Similar types of information about other diseases and insects may contribute to changing the emphasis in existing programs, or to the establishment of new ones. The test plantings provide additional alternatives in the search for resistance, which formerly depended more on heavy infestations and epidemics in natural stands or plantations. I expect a considerable expansion in efforts to produce varieties with built-in resistance, especially in view of the public's growing concern about all types of pollution, including pesticides, in our environment.

Effectiveness of Selection

The methods used in finding and testing resistance are becoming much more complex. The sophisticated techniques that are commonly employed have diverse influences on a breeding project. They may include dignifying research plans, attracting support for research while adding to the cost, and glamorizing publications. Hopefully, they also help us to gain a deeper understanding of the complicated host-pest-environment relationships, and improve the selection process.

Although the selection of supposedly resistant phenotypes in the forest is beset with uncertainties, certain of these can be reduced. Van Arsdell (1965 a and b), for example, has greatly refined the knowledge of the microclimate and epidemiology of white pine blister rust. Silver iodide tracers, wind tunnels, and tagged spores are to be used in further studies. Patton and Riker (1966) have taken advantage of this information about blister rust distribution patterns in making their recent selections.

The use of artificial inoculations for making comparisons of disease resistance has become nearly a standard practice, at least in progeny testing. It has been employed with fusiform rust (Driver et al 1966, Goddard & Arnold 1966, Jewell & Mallett 1964), **Fomes Annosus** (Driver & Ginns 1966), littleleaf disease of shortleaf pine (Bryan 1965), white pine blister rust (Hoff 1966), Dutch elm disease (Ouellet 1964), and others. Some procedures simulate conditions that could occur in nature, while others are quite different. In the littleleaf work, for instance, two-to six-week-old seedlings were employed in separate test tubes that were plugged with cotton. Although techniques vary, they generally tend to employ small trees in large numbers, uniform and sometimes repeated inoculations, and a dosage that permits optimum discrimination of resistance levels.

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Problems may arise in attempting to obtain uniform and repeatable results. Information about spore distribution and germination has been obtained by using phosphorus - 32 (Pomerleau & Mehran 1966) or fluorescent dye (Patton 1967). Changes in soil moisture partly explain seasonal variations in susceptibility to Dutch elm disease. (Smalley & Kais 1966). Studies such as these help to define optimum conditions and to improve the reliability of testing.

Selection for insect resistance involves further complications, introduced through variations in insect behavior. In the case of the Douglas fir beetle (Atkins 1966), changes were noted in a population as the season progressed and from year to year due to both innate and environmental factors; host-positive females behaved differently from those that tended to fly away.

It is especially desirable to have a thorough understanding of insect behavior when artificial infestations are employed to screen for resistance, in order to avoid the possibility of deviations in the effectiveness of testing. The rather large variability in natural insect attacks is one of the main reasons why artificial exposures are so useful. We have been able to find differences in susceptibility to white pine weevil attack among white pine provenances by exposing seedlings in cages, even though there were only ten trees per provenance, and these were shorter than trees ordinarily attacked in nature (Soles and Gerhold 1967). Results from older white pine provenance experiments had been much less revealing.

Smith (1966) is developing a method of forcing attacks of western pine beetles to test the resistance of pines, which appears to be influenced by resin composition. The beetles can be restricted to individual trees by cages, or an indigenous population can be attracted by hanging freshly infested ponderosa pine bolts just below the crown. If these field tests confirm the laboratory findings which suggest that certain resin components confer resistance by the lethal effect of vapors on attacking insects, the breeding of resistant varieties will be facilitated. The resin of a phenotypically resistant tree can be analyzed quickly by gas chromatography, in order to classify it for a mating design. We are using similar techniques to study the olfactory reactions of weevils to the terpenes of white pines.

Other studies are uncovering additional effects on insects related to chemicals in their hosts. A volatile principle from oak leaves is prerequisite for the release of sex pheromone by the female Polyphemus moth, which is necessary for the sexual activation of males (Riddiford and Williams 1967). A compound isolated from balsam fir prevents hemipteran nymphs from becoming sexually mature (Bowers et al 1966). Three terpene alcohols isolated from the frass of male bark beetles have been identified as the sex attractants responsible for the mass attack following initial boring activity (Silverstein et al 1966).

In view of so many fascinating possibilities for research, it is well to keep in mind that not all of them will contribute directly to progress in improving trees. If a diversion of resources into a tangential line of research is contemplated, its potential contribution to improvement objectives should be assessed carefully.

Useful Life of Resistant Varieties

There continues to be concern about the possibility of pathogens and insects overcoming improvements in the resistance of trees. Some limited evidence has been accumulating that pests are capable of adapting to new hosts, and of course agricultural breeders are well aware of the problem. Holmes (1965) has discovered differences in virulence among several cultures of the Dutch elm fungus; both virulence and resistance apparently involve polygenic inheritance. Different forms of **Cronartium fusiforme** have been reported (Kais 1966), though I do not know that they differ in virulence.

The genetic variation that is prerequisite for adaptation to a new or more resistant host could be introduced through hybridization. The white pine weevil is capable of crossing with related weevils (Manna and Smith 1959, Drouin et al 1963, Godwin and Odell 1966), and this could provide one possible explanation of how it was able to adapt to red pine in Michigan (Graham and Satterlund 1956). Lewontin and Birch (1966) have described a situation in Australia in which hybridization apparently provided the variation that enabled an insect to extend its adaptation to new hosts and environments.

The experience of wheat breeders in Mexico could lead us to make pessimistic predictions, if an analagous situation existed in forestry. Six different stem rust races have occurred in 20 years, so that a useful lifetime of only 4 years is expected for a pure-line wheat variety. In temperate zones, where ecological conditions are less favorable for the rust, the useful lifetime is three times as long (Borlaug 1965). Fortunately, most tree species are much more heterozygous. In addition, a variety of measures can be taken to make it more difficult for a pest to overcome resistance. Further research is essential so that we will know which of these measures may need to be taken.

Personnel and Communications

Few, if any, resistance breeding projects have adequate personnel and resources for the development and production of tree varieties with improved disease or insect resistance. In view of this situation, collaboration and communication among those having common interests is especially important. Considerable efficiency can be gained by exchanging information and ideas, sharing biological materials, and possibly joining forces or dividing responsibilities to accomplish certain phases of the work. For some years tree improvement conferences, workshops, regional research committee meetings, and various other regional, national, and international meetings have been successful in improving communications.

The need for more direct contacts among geneticists, pathologists, entomologists, and physiologists has been felt by many individuals. Resolutions to this effect were passed at the World Consultation on Forest Genetics at Stockholm in 1963 and at an Advanced Study Institute on Genetic Improvement for Disease and Insect Resistance of Forest Trees in 1964 at the Pennsylvania State University. As a result, the International Union of Forest Research Organizations has organized a Working Group to deal with this subject. It is open to all interested members, and will be organized more formally at the 13th Congress in Munich this year. The main objective will be to facilitate cooperation among those persons who are working on resistance to particular diseases or insects, by improving communications among indivudials, and by organizing specialized symposia.

Conclusion

In looking toward the future, I see many opportunities for practical improvements in disease and insect resistance. We have fairly good knowledge of the complexities involved in selection, and we are developing workable techniques to cope with them. We still have much to learn about breeding systems that will produce the improved varieties. This is one of our most urgent needs.

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Maximum Use of Minimum Acres

JOHN E. KRAJICEK [1]

There was a time, not long ago, in the geologic time scale, when not one acre of the 56,790,000 square miles making up the seven continents was claimed by a human being. Less than 400 years ago, our country was shared by a few hundred thousand Indians. Today, the 2-1/3 billion acres in the United States are shared by about 198 million people, an average of less than 12 acres per person. And this average is shrinking fast.

How is this area allocated? Some of the major uses are urban developments, crop farming and livestock raising, highways, railroads, power line rights-of-way, water impoundments, parks, wildlife preserves, wilderness areas, and productive forests. This does not leave much of the 12 acres available for any single use.

Our concern here is the productive forest, which I define as the segment economically providing the raw materials for wood-using industries, ranging from pulpwood production to face veneer of fine hardwoods.

Is our timbered area holding its own against the demands from other uses? On strictly an area basis, the situation is not bad; the area has decreased only 8 percent since 1900. But area does not tell the whole story. Many acres not timbered then are now forested, whereas even more land then forested has since been cleared.

Some examples will illustrate this shift. In Arkansas, from 1935 to 1950, there was a 19-percent reduction in the timbered area in the Delta portion. During the following 8 years the timbered area for the state as a whole increased about 7 percent, but in the Delta portion it decreased another 7 percent.

In Mississippi, the timbered area increased between 1948 and 1957 by 4 percent, whereas in the Delta region it decreased 6 percent.

In the Prairie region of Missouri, the timbered area increased 15 percent between 1947 and 1960, but in the Riverborder region it decreased 7 percent. Even more striking, for the six Bootheel counties within the Riverborder region, the decrease was 39 percent for the same period.

Thus, highly productive timber land has been cleared for agricultural use and less productive acres have replaced these good lands in the total forest land inventory. Economically it is difficult to argue against this change. However, the trend does point out the need to get maximum production from each acre, with the greatest emphasis on the better sites still available. In a sense, we must make each acre bigger.

There are many ways to increase production. The simplest and least productive, extensive silviculture, and one requiring little or no investment, relies completely on natural reproduction with little concern for species composition. At the other extreme, we can rely exclusively on planting, where we can control spacing, species composition, and the use of improved trees within a species, and can more easily apply stand improvement measures such as pruning, fertilization, irrigation, and weed control. On the better sites these intensive practices will likely become more and more commonplace.

A major step in increasing production on the diminishing acres can be made solely by exerting greater control over stand composition. For example, probably no one has ever retired comfortably on the profits from harvesting boxelder, but much has been invested to eliminate it from stands so that better trees will have more growing space. Sixty percent of the current hardwood sawtimber growth is concentrated on less desirable species, such as hickory, beech, and inferior upland oak species. Certainly the land owner whose income is solely from such timber had better look into alternative land uses.

Production can be increased also, at least for some species, by fertilization, weed control, and irrigation. But none of these benefits can be fully realized if adequate growing space is not provided, whether in plantations or natural stands.

Many trees have been wasted simply because an acre cannot support as many large trees as small ones. So, many of the trees are removed either by natural mortality or by noncommercial thinnings or poisoning. In addition to this direct loss there is another important one: through competition the wasted trees have reduced the growth of those that will make up the harvest.

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The major reason for wasted trees is that until recent years we did not really know how much space a tree of a certain size and species could use. So we either left or planted enough per acre so that we could be sure of having enough for the harvest.

Fortunately, it is a relatively simple matter to determine how much growing space a tree can use. This was first shown for several oaks, hickory, and Norway spruce, where very high correlations were found between crown width and d.b.h. Since then the same high correlations have been found for several conifers in Canada, eucalyptus in Australia, and a number of conifers and hardwoods in this country.

One thing should be emphasized at this point. Despite the highly correlated relationships, the crown width in relation to d.b.h. can vary greatly among species (Table 1). The differences are even more striking when the widths are converted to crown area. For example, for 15-inch trees the crown width of Norway spruce is 81 percent of that for oak-hickory, but the area of the crown is only 59 percent of that for the oak-hickory. Consequently, far more trees and volume can be produced per acre with one species instead of another, assuming equal site suitability and comparable diameter growth rates.

Table 1.--Equations for Crown Width of Open-Grown Trees

Species	Y = crown width in feet D = d.b.h. in inches	Basis: no. of trees	r^2
Black walnut[1]	Y = 1.993D + 4.873	36	.98
Oak-hickory[2]	Y = 1.829D + 3.12	173	.97
Norway spruce[2]	Y = 1.313D + 5.057	157	.98
Lodgepole pine[3]	Y = 1.424D + 3.27	--	--
Eastern white pine[4]	Y = 1.714D + 2.54	69	.91
Austrian pine[4]	Y = 1.442D + 3.72	145	.97
Sweetgum[4]	Y = 1.975D + 2.65	46	.93
Baldcypress[4]	Y = 2.026D + 8.32	47	.89
Pin oak[4]	Y = 1.525D + 9.06	41	.91
Sycamore[4]	log Y = 0.6428 (log D) + 0.8341	64	.98
Jack pine[5]	Y = 2.036D + 1.763	83	.92
Loblolly pine[6]	Y = 1.56D + 4.78	600+	--

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2/ Krajicek, John E., et al. Crown competition--a measure of density. Forest Sci. 7(1):35-42. 1961.

3/ Alexander, Robert T. Site indexes for lodgepole pine, with corrections for stand density. U. S. Forest Serv. Res. Pap. RM-24, 7 pp. 1966. Rocky Mountain Forest and Range Exp. Sta., Ft. Collins, Colo.

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There is another aspect that must not be overlooked. In addition to the differences among species in the crown width-d.b.h. relationship, there are differences in how trees of various species react when crowns close and crowding begins. Though sycamore has the widest basic (open-grown) crown of any hardwoods investigated so far, stands with high basal area and volume per acre are found. On the other hand, oak-hickory stands with a narrower basic crown have basal area values per acre that do not exceed or even come close to sycamore. What is not known, however, is whether the percentage reduction from the maximum growth rate is the same for heavily-stocked oak-hickory and sycamore stands.

It is reasonable to assume that growth (total production of dry matter) will be greatest in the open-grown tree. As the trees are brought closer together, the crowns will finally touch and eventually become crowded so that there will be a reduction in actual or effective crown size. This will result in a reduced production of dry weight per tree. In the final analysis, the dry weight production per acre of living trees will be reduced also.

With the characteristics of open-grown trees known, one can predict, for any initial spacing, the size (d.b.h.) of the trees at the time the stand begins to close. For one interested in rapid growth of individual trees to a specific size, this is a crucial point, particularly when crown width varies with d.b.h. among species.

For example, we may want to have the stand start closing at d.b.h. of 5 inches for sycamore, white pine, and loblolly pine. From the equations in Table 1 we can compute the following initial spacings (rounded to the nearest half-foot): sycamore, 19 x 19; white pine, 11 x 11; and loblolly pine, 12.5 x 12.5.

In our work with black walnut, using open-grown tree data and with an objective of rapid growth until harvest, we have decided that a spacing of 18 x 18 feet is needed to produce sawlogs, and a spacing of 26 x 26 feet to produce veneer logs. We recognize that some pruning will be necessary. And possibly a pulpwood crop of another species can be produced among the walnuts during the first half of the rotation without detriment to the walnut. We believe this will give us maximum use of minimum acres.

It is not difficult to collect the basic data needed to apply this approach to spacing. The standards we have used in selecting our sample trees are:

1. Crown free of competition on all sides.
2. Limbs extending to the ground on small trees and nearly so on larger trees.
3. Lowest branches the longest, or at least as long as those above. (This eliminates trees that had been released from competition in the past and on which the lower portion of the present crown originated from epicormic branches.)
4. For small trees (less than 16 feet tall), no forking in the entire length; for larger trees, no forking of the bole below 16 feet. (This limits the sample to trees that are of the type that would be favored in the forest stand, except for limbiness and excessive taper.)
5. No evidence of pruning, shearing, browsing, decadence, storm damage, or serious insect damage.
6. Tree apparently not of sprout origin.

Tree diameters are measured to the nearest tenth-inch and crown widths (the average of two measurements) to the nearest half-foot. With careful adherence to the standards of sample tree selection, relatively few sample trees (50 or less) may be adequate.

The characteristics of open-grown trees can also be used to decide on the initial spacing where one or more intermediate cuts are planned. In fact, the characteristics provide an excellent guide to prevent overthinning. Understocking is just as much a factor in production loss as overstocking.

This approach, using initial wide spacing, is contrary to what many foresters accept. However, we feel that, where the product objective is sawtimber, this procedure will provide the most of the desired product in the shortest time. Intensive culture, such as pruning and weed control, will be necessary. This is not the easiest way to practice forestry, but we believe it is the quickest way to get increased production of desired products.

New Silvicultural Methods

CHARLES D. WEBB and ROBERT G. McALPINE[1]

When we tried to decide which silvicultural methods to discuss as being "new", we set 10 years ago as the dividing point between "new" and "old". But we could not think of a truly new silvicultural method proposed during the past 10 years. Fertilization of forest trees has been tried for many years; only the aerial application of fertilizer seems to be a new wrinkle. Coppice regeneration of hardwoods, which has received renewed interest lately, is an ancient practice. Clear-cultivation of plantations is not new. If our silvicultural methods are not new, what then is "new"?

The most important "new" factors are the present and future social and economic conditions under which we must practice silviculture. Sky-rocketing taxes and labor costs, the scarcity of labor, and pressures from land-use systems are some of the new developments that are affecting silvicultural decisions. These pressures will force us to find new combinations of old silvicultural methods. Some of these new combinations may grate against our sense of propriety as foresters. But we must be willing to use them if we are to achieve the most efficient and profitable use of the land available.

We have chosen two recent silvicultural developments to discuss today. The first is the increasing availability of improved seedlings from seed orchards; we as foresters should find this very comforting. The second may shock our sense of propriety; that is, the recent proposal called silage sycamore (McAlpine et al., 1966). This is actually a silvicultural concept rather than a silvicultural method.

Seed Orchard Seedlings

We have heard repeated references today to the progress made in southern pine tree improvement programs during the past 16 years. Several million seedlings have already been produced from the seed orchards. More seedlings will be available from orchard seed next year, and even more the year after that. As they become available, these seedlings are being incorporated into routine planting programs using the same site preparation and spacings that are used on unimproved planting stock. In most cases, there is no post-planting cultural treatment, such as fertilization. Should they be planted with no extra care, or can more intensive cultural practices be used economically on the improved stock?

In agricultural crops, the development of new varieties has accompanied improvements in cultural methods. These agronomic advances have involved land preparation, planting methods, stand structure, fertilization, and chemical control of diseases, insects, and weeds. Increased mechanization has been an integral part of all these changes. The result has been a reduction in total labor requirements as well as an increase in the productivity of each cultivated acre.

For forest trees, evidence is mounting to indicate the existence of strong interactions of clonal and seedling lines with cultural treatments (Walker and Hatcher, 1965; Curlin, 1967; Pritchett and Goddard, 1967). In most instances, intensified cultural treatment has been simply the application of fertilizer, although some studies have included post-planting cultivation for weed control and irrigation. Consequently, the university-industry cooperative tree improvement programs in Florida and North Carolina are beginning to incorporate fertilization into their plans for progeny-testing seed orchards. They are doing this to identify those lines that respond the most to fertilizer as well as those that do well with no extra treatment. Hopefully, these interactions of genotype with cultural practices can be exploited fully by controlled breeding.

A number of intensive care studies are also being put in, using bulked lots of seed orchard seedlings. One such study, by Georgia Kraft Company is attempting to achieve maximum growth of loblolly pine seedlings from orchards of the Georgia Forestry Commission. Seedlings receiving the intensive treatment were center-planted in holes dug with a motor-driven portable post-hole digger. Since planting, the intensive care plots have been fertilized twice a year, disced once a year for partial weed control, and irrigated intermittently. BHC and Thimet have been applied for tip moth control and Ferbam for fusiform rust. Seedlings on the check plots were planted with a dibble but have received no additional cultural treatments. Similar but less intensive studies are underway within the North Carolina State University program.

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All of these intensive care studies are still too young to allow any firm conclusions about the over-all effects of intensive care on growth and ultimate profit. In most of these studies--probably in all of them--intensified cultural treatment has meant an increase in total labor requirements. However, the labor situation is already so critical in some areas of the country that intensified cultural treatment on a large scale would be impossible even if it were known to be economically desirable. Consequently, our silvicultural research in the future should emphasize two important areas. First, it should identify those improved lines that will respond to cultural treatment as well as those that will do well with little or no extra treatment. Second, silvicultural systems must be developed that will integrate, in economical combinations, tree breeding, cultural treatment, and mechanization from site preparation through harvest.

"Silage" Sycamore

While attending the Eighth Southern Conference on Forest Tree Improvement at Savannah, McAlpine **et al.** (1966) put together a silvicultural concept they called "silage" sycamore. They were deeply disturbed by skyrocketing taxes and labor costs, by harvesting problems caused by scarcity of woods labor, and by the economic consequences of compounding costs over rotations of 30 years or longer. As a partial solution to these problems, they envisioned growing trees at rotation ages as short as two or three years and mechanical harvesting of whole trees--trunk, limbs, bark, and perhaps even leaves. The harvesting machine would be similar to, but larger than, a conventional forage or silage harvester. In a continuous operation, the harvester would cut the tree, chip the entire tree, and blow the chips into a wagon for movement to a central loading point.

The proposal includes:

(1) Planting or direct seeding a fast-growing hardwood such as sycamore at spacings as close as 2 x 2 feet or 4 x 4 feet.

(2) Mechanical harvesting as early as two or three years of age.

(3) Coppice regeneration.

(4) Repeated harvest and coppice regeneration until the sprouting ability of the stumps drops below an acceptable level.

The wood produced in this operation is strictly juvenile wood, but it has many potential uses. Preliminary tests of paper made from whole five-year-old sycamore trees (trunk, limbs, bark, and leaves) are very promising. In properties such as bursting strength, tearing resistance, and tensile strength, the sycamore paper compared well with paper made from three commercial pulps: northern softwood kraft, southern softwood kraft, and northern softwood sulfite (acid process). This pulp will probably be most valuable as a substitute for present hardwood pulps in mixtures with long-fibered pulp.

On a very limited scale, whole five-year-old sycamore trees (trunk, limbs, and bark) have been made into particle board. Preliminary strength tests were encouraging, but some problems also became evident. These tests are being continued.

These preliminary tests on five-year-old sycamore trees were limited. To establish fully the utility of juvenile wood of the numerous hardwood species that might be grown under this concept, each industry concerned should run its own tests to see where this type of wood can be incorporated into its product line. Processing methods may or may not have to be changed to handle this wood.

As a system for producing wood fiber acceptable for certain products, the "silage" sycamore concept has much to recommend it. First, mechanization and low labor costs are the key words from planting to harvest. The machines needed to harvest saplings should be cheaper to build, lighter, and capable of operating on a wider variety of terrain than those required to harvest conventional pulpwood. Second, short rotations should be, in some respects, more profitable than long rotations in an age of high interest rates and increasing taxes. Third, the ability of hardwoods to regenerate by stump sprouts and root suckers seems to promise that a single planting may suffice for three or more rotations. Fourth, preliminary estimates indicate that total yields per acre in tons of fiber over an extended period will exceed those produced by pine on conventional 30- to 35-year rotations. Finally, tree improvement by selection and controlled breeding should be a powerful tool in implementing this concept. We should be able to create relatively quickly special, improved strains for short rotations and coppice regeneration.

In spite of the promise that this concept offers, we must be careful in our research and restrained in our enthusiasm to put it immediately on a production basis. We must not over-estimate the value of the concept, but even less can we afford to under-estimate its value. Many questions remain unanswered. Maybe after 10 or 15 years of thorough research, we can put this concept on a production basis. By then, our research should enable us to make recommendations on species, sites, site preparation, planting or direct seeding, spacing, weed control, disease and insect control, fertilization, rotation ages, harvesting machinery, special improved strains, expected yields, and suggested end products. Each of these points will require a major research effort.

At best, the "silage cellulose" concept will supply only part of our needed cellulosic raw materials. It should, however, become an integral part of the over-all picture by alleviating the drain on hardwoods by certain pulp products and allowing these trees to go on to other products requiring larger size and better quality, such as veneer and lumber.

Silviculture of the Future

What will typify our silviculture of the future? Certainly, intensive cultural methods, genetically improved strains, and mechanization will become prominent features of future silvicultural systems. In addition, these systems of the future will most likely emphasize a broader concept of wood quality than present systems.

Seidl (1965) proposed such a broad, practical concept of wood quality for the future: "*...quality over a period of time is a changeable attribute that is characterized by a dynamic balance among intrinsic properties, economic value, and consumer satisfaction.*" Also, "*...wherever wood exists in quantity, in concentrated form, and at lowest cost, the force of technology will be applied to make useful products for the population.*" That is, the wood available and its cost will create a standard of quality. But Seidl also urged, "*...we should continually aspire to achieve the maximum volume and weight of wood in trees of good form on the minimum number of stems.*"

This is a broad concept of wood quality. It definitely includes the ideas on wood quality that were emphasized in the systems used to select the parent trees in our current seed orchards. But the concept is broad enough to include the recently proposed 'silage sycamore' or 'silage cellulose' concept. This view of wood quality and the pressing need for mechanization will greatly influence the new combinations of old silvicultural methods that we will use on our genetically improved planting stock in the future.

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Comparison of Tree Improvement Programs with Crop Breeding Programs

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The title of this talk may appear presumptuous, if nothing else. The hazards of comparing improvement programs with plants as diverse as a loblolly pine and an alfalfa plant at first appear formidable, if not insurmountable. One thinks immediately of the obvious differences in plant size, longevity, generation time, management conditions, etc. From the standpoint of geneticist and breeder, however, these differences are essentially superficial, while in fact the intrinsic similarities between an alfalfa plant and a southern pine are also rather formidable. Both are highly cross-pollinated and rich with native heterogeneity; interspecific compatibilities in each species afford an immense germplasm within reach of the breeder; both crops are bred for maximal productivity with less immediate concern for "type" (as, e.g., in breeding apples); both are long-lived and have unique parasitic and pest problems stemming from this longevity. Perhaps the only real hazard lies in carrying this kind of thinking too far!

Most forest trees are highly outcrossed, some as a consequence of genetic self-incompatibility, and most of them show almost exasperating interspecific compatibilities. Progeny tests reveal extensive genetic variability even from limited and more or less homogenous provenances, a fact which is probably not fully appreciated by silviculturists, forest soils enthusiasts, etc. Rapid and exciting genetic gains have been made in forest breeding during the past decade, especially in the southern United States, capitalizing on this variability through selection and breeding. But a second stage, or a second cycle of improvement, has arrived for the major forest species of the southern United States. With new methods increasingly available to accelerate tree generations, the breeder is or soon will be in his advanced generations of improvement. Few crop breeders have more than a passing acquaintance with this exciting decade of genetic advance in forest tree improvement. Thus it becomes encumbent on the forest breeder to draw his own lessons from the foibles and bobbles of breeders and geneticists working with other, more intensively studied organisms. The fact that I was invited to attempt such comparisons today indicates your confidence in your ability, at least, to profit by the experiences and errors made in this past half-century of intensive breeding advance with other crops.

I've chosen to organize my comments into a series of **significant current trends** in research in plant breeding and genetics, and attempt to relate them, where possible, to forest breeding problems. It will be obvious that I feel that some of these trends are highly oversold or even irrelevant, while others are long overdue and have not yet been exploited adequately by the breeder.

1. THE TREND AWAY FROM CLASSICAL TYPE

First, there appears to be a strong trend away from what I have chosen to call classical type. Breeders have become increasingly aware of the fact that maximum yields under cultivation are obtained on plants that bear little resemblance to those grown by the farmer, or to those which nature appears to have favored. An interesting example has been given today in the "silage sycamore," being cut every 2 to 3 years for pulpwood, much as one would a forage crop.

I will long recall a newspaper photograph of famed President Magsaysay of the Philippines, standing proudly in a rice field with an eight-foot rice plant towering over him, a vigor long symbolic of high yields to farmers and agricultural scientists alike. Now, at Rockefeller's International Rice Research Institute in the Philippines they discard, as useless, plants over three feet tall. Maximum yields are obtained from day-length insensitive dwarfs selected for high nitrogen response, and this is for regions in which rice has been grown without fertilization for centuries! This story was born in a geneticist's intrigue with radiation-induced **erectoides** dwarfs, reaching its fruition in a revolutionary era of dwarf sorghum breeding. Today it extends to many crops, including corn and vegetable crops; in each case, the trend is toward increased use of fertilizer, increased plant populations, genetic dwarfing of vegetative portions of the crop and selection for non-response to day-length variations.

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Farmers, plant physiologists, and consumers often have encouraged or compelled breeders to breed within a classical type, partly on the age-old philosophy that nature must have done it that way for a purpose. Of course, an eight foot tall rice plant does compete better in paddies full of weeds, with uncontrolled flooding and no fertilization, but the cultivated crop simply cannot be grown as it was in jungle or neglected pasture.

Most plants are vastly more efficient photosynthetically than they need to be; rice physiologists now tell us that only two healthy leaves can produce enough photosynthate for a plant's entire seed crop. Similarly, plants are often more reproductive than the crop demands, flowering and fruiting abundantly with its consequent drain on vegetative yields. These traits may make a plant compete well in nature, or under conditions of inadequate care and fertilization, but are unnecessary or even detrimental to the cultivated crop.

An example with which I am most familiar occurs in the tropical woody legume, **Leucaena**, which is most commonly found as a pantropical, abundantly flowering, vigorously weedy shrub. Simple selection of non-flowering types from the center of origin of **Leucaena** in Mexico lead to doubling or trebling of forage yields under management. When these non-flowering plants are not harvested, they grow into a handsome tree, not a shrub, attaining over 30 ft. of growth in two years in Hawaii; a potential dual purpose forage-forest plant.

This trend away from classical type received impetus long ago with the recognition of corn breeders that maximal yields were not obtained when selection favored those long, beautiful ears which won prizes at the State Fair. It seems to me this trend away from classical type will see real development as forest tree breeders exploit genes for yield. A tree bred for pulpwood or presswood need bear little resemblance to the same species bred for sawtimber; breeding of non-flowering or sterile hybrids almost certainly would increase vegetative growth in some species; crown shape should be susceptible to dramatic dwarfing without effect on per plant yield but permit greater plant populations, and you could suggest many other examples.

2. THE TREND AWAY FROM PURE LINES

A second trend which I would like to consider is the trend away from pure lines, and from the homogeneity achieved by prolonged inbreeding or clonal reproduction. This trend is more like a hasty retreat in the cereals, where new mutant races of plant pathogens have forced the breeder to consider new approaches.

Drs. N. Borlaug, N. Jensen and others have long expressed concern about the wisdom of widespread use of pure lines in the self-pollinated cereals, and Syrach Larsen, among others, has expressed a similar concern regarding the use of clones in forest plantings. At the 2nd Forest Genetics Workshop (1964) Dr. Borlaug described his multilineal approach to the cereal breeding problem, allowing the population wide genotypic variability with respect to rust resistance, while maintaining the requisite homogeneity in type. Even corn breeders appear to be retaining greater genetic variability in their varieties and inbreds, especially in the tropics where the pathogenic flora is year-round. Every plant breeding student is familiar with the story of rust race mutations, so I won't belabor it. Its impact on pure line breeding has been greatest in relation to self-pollinated crops and their obligate parasites, particularly where resistance is monogenic. Its relevance to forest tree improvement may be limited.

The major bearing of the trend away from homogeneity on forest breeding might be in the use of clones, as in many hardwoods. An interesting example is obtained in breeding of sugarcane clones at the Hawaii Sugar Planter's Association. Each new clonal variety remains in production for a period of about 15 years, by which time a yield decline, small but significant, has set in. The decline is attributed to the gradual buildup of microflora and phytotoxins, both externally and internally in the roots. Changing clones resolves this problem for the sugarcane breeder, but imposes a continual drain on the resources of the breeder (c. f., Borlaug, 1964).

A clone is clearly more susceptible to the hazards of catastrophic loss to disease and ecologic or climatic disasters, but similar catastrophies are not uncommon at the racial or species levels. Against this problem stands the elegance of clones from the breeder's standpoint, and of their advantage in rate of breeding advance. One cannot but marvel at the intrinsic buffering capacity of single clones in trees such as Cryptomeria in Japan, or commercial varieties of the apple and cherry. The weight of evidence probably favors the ultimate use in forest breeding of synthetics, single crosses or otherwise more heterogenous populations, permitting greater buffering ability to those unforeseen variables of site, climate, and parasites. However, the prospective rate of genetic gain with selected single clones may make their use in early stages of the breeding program most attractive.

3. THE TREND TOWARD REEMPHASIS OF THE SIGNIFICANCE OF SINGLE GENES

Plant breeders often deplore the inadequate training in quantitative genetics gained by today's students, since many genetics courses hardly mention polygenic traits. But one can also deplore a common failure of plant breeding courses to emphasize the dramatic effects which single loci may have on a crop; animal breeders are more cognizant of this than we, with their chondrodystrophic dwarfs, featherless fowls, etc.

Corn geneticists have known for almost 3 decades, about 50 genes affecting the maize endosperm and seed tissues. Biochemists largely ignored them, while breeders regarded them in a class with scute bristles and apricot eyes. Now, one of these genes, opaque-2, has been found to raise the lysine level in the corn seed, giving corn a balanced protein of exceptional nutritional value that can be fed as complete diet to animals. This single gene promises to revolutionize the use of corn throughout the world; since the 1930's it has been just a genetic marker. Today, it appears in the speeches of our Secretary of Agriculture. Many other striking examples of single gene loci, often obtained at considerable expense by the breeder from distantly related species could be cited, such as the dwarfing genes or the determinate flowering genes that permit mechanical harvesting in tomato.

Regrettably, breeders usually study monogenic traits more or less incidentally, because they happen to segregate, or because one of our students wants to see a real 3:1 ratio. Perhaps we are long overdue to seek and study carefully the monogenic variants affecting economically-important traits. In India today, they are screening the world collection of sorghum (over 10,000 varieties) for opaque-like mutants with the high-lysine property. It may have elements of an Edison patiently trying thousands of metals; but then, one cannot question Edison's contribution, either.

4. THE TREND TOWARD USE OF SINGLE-CROSS HYBRIDS

A third trend, if it may be called that, is toward the universality of controlled single-cross hybrids. This is an historic trend, with significant recent additions in the hybrid sorghums, alfalfas, wheats, sugarbeets, cottons, onions, cabbages, and ornamentals. It is a trend often dependent on genetic tools like cytosterility and restorer genes, or self-incompatibility. While it may be immediately applicable to trees like the SI sweetgum and yellow poplar, its application to pines or oaks, for example, may be something else. Perhaps a serious search, however, for cytosterility in gymnosperms would pay off in less time than one might expect.

In corn breeding, the current shift to single-cross hybrids represents a move away from the traditional double-cross hybrids. This has occurred largely since the use of single crosses permits more rapid genetic advance, with only two parents to be altered vs. 4 for the double cross. The corn breeder has been obliged to improve the vigor of his inbreds as seed parents for single crosses, using sib matings with more careful tests of combining ability in lieu of intensive and prolonged self-fertilization. It has become apparent that judicious selection during gradual inbreeding can produce extremely vigorous, high yielding inbreds; the weak, spindly little corn inbreds of our text books are almost a thing of the past.

Single crosses are not yet fully exploited in many crops, such as the forage crops, where there is less value of homogeneity of the cultivated crop. Nonetheless, the trend to single crosses reflects an underlying sense of the generality of the significance of specific combining ability – of the extraordinary interactions of specific single genomes – that is best capitalized upon by the single cross. I think we are on the threshold of some biochemical evidence, from hybrid enzymes, for epistatic and overdominance contributions to heterosis that will enforce upon us the significance of breeding to maximize use of specific combining ability.

5. THE TREND TOWARD USE OF GENETIC DISEASE AND PEST RESISTANCE

Rachel Carson's "Silent Spring" gave renewed impetus to another trend in plant breeding, that of increasing emphasis on genetic resistance to diseases and pests. A major element of this trend deserving our review, is that of monogenic vs. polygenic sources of resistance. Outwardly, the trend might appear to be away from monogenic resistance, and is most evident again in breeding for rust resistance in self-pollinated cereals.

Walker (1964) has emphasized, however, that many forms of dominant, single gene resistance have held up very well without the evolution of new virulent forms; e.g., the resistance of peas and tomatoes to **Fusarium** wilt, of cucumbers to cucumber mosaic and bacterial wilt, and of corn to **Helminthosporium** blight. Classically, these have been single genes which confer a mature plant resistance serving as a check to the pathogen while not inhibiting it completely. The view is encouraged that selection for mature-plant resistance may circumvent the hazard of catastrophe associated with selection for antibiotic immunity. It is always tempting to favor a plant which escapes symptoms entirely; we are perhaps wise to favor seedlings which coexist with a pathogen but fail to succumb to it.

Exciting strides are being made in understanding the biochemistry of disease and insect resistance, and these may be expected to shed light on the breeder's approach. Phenolics and polyphenoloxidases have been associated with resistance to many pathogens (e.g., pinosylvin in blister-rust resistant pines, phloridzin in **Venturia** resistant apples, and other phenolics in resistance of **Beta** to **Cercospora, Daucus** to **Ceratocystis, Solanum** to **Phytophthora** and **Triticum** to **Puccinia**). Isoenzymic approaches, to be described, provide additional potential for understanding pest resistance.

Forest breeders often have the opportunity to exploit genes for resistance that are widely dispersed in the genera with which they work, and this leads me to my next trend.

6. THE TREND TOWARD BROADENING GENE BASE FOR IMPROVEMENT

We have been wisely tutored in the hazards of wide crosses, with emphasis on the mule and his sterility. Plant breeders have demonstrated, however, that the major value of wide crosses within or outside the species is in terms of the genetic bridge that they offer for transfer of desirable gene blocks, not in their use **per se.** We may be impressed with the great difficulty of transferring a given gene, e.g., from the diploid **Triticum aegilops** to highly-selected inbred varieties of hexaploid wheat. At the same time, the problem is different with highly heterogeneous forest trees or forage crops, for example, where a little sterility is of no great concern.

Forest tree breeders can provide exciting examples of this trend to broadening gene bases for improvement, since the interspecies fertilities of forest trees are striking, and the breeder is not so completely dependent on seed or fruit production. Some species crosses in forest trees are of potential value **per se,** as the slash x shortleaf pine crosses. It is fascinating to read of interspecific crosses, for example, that allow a forest breeder to transfer genes from the Torrey pine, through genetic bridges like the Coulter and Jeffrey pines, to the Ponderosa, or **vice versa.** Evidently the Southern pines are a little more discriminating in their tastes, crossing only with other Southerners, but the scope of usable genetic variability is nonetheless staggering.

I'm well aware that the breeder is soon buried under an avalanche of apparently worthless provenance or species crosses, and it is difficult to convince administrators that all this interspecific junk in the nursery is really worth keeping. Still, I think we should resist efforts to turn aside these interspecific and inter-provenance crossing studies, so long as they do not displace the intra-species programs entirely.

Recognizing that many of our plant species are rapidly disappearing from natural vegetation, the emphasis on germplasm pools has arisen. Clearly, one should preserve seeds or frozen pollen of all forest species crosses, although they might appear of no immediate value, and I hope that some sort of gene bank has been established to this end.

7. THE TREND TO LARGER POPULATIONS FOR SELECTION

Related to the trend toward broadening gene base is a concomitant trend of enlarging the populations on which selection is initially practiced. It is often almost ridiculous how small the initial populations for a selection program are, and little wonder indeed that such trivial progress is achieved. Even with minimal inbreeding, the average breeder would be faced with near-extinction of his materials if he threw out everything he'd prefer to, emphasizing the value of large initial populations in early stages of selection.

Sugarcane breeders in Hawaii, recognizing the great heterogeneity of their material, with its polyploidy and multi-specific base, select about 1000 seedlings a year among over 2,000,000 grown, for an index of selection of about ½%. With clonal increase and evaluation the second year, this selected sample diminishes another 95%. Clonal increase is a powerful tool in selection, but much more so when initial selections represent a truly elite fraction. As an aside here, the sugarcane breeder has a problem with sporadic self-pollination similar to that, for example, in open crosses of pines (e.g., shortleaf x slash), but they choose to ignore natural selfs on the pragmatic stance that if one ever did survive their intense selection, it must be worth evaluation.

Probably no field of plant breeding is currently so preoccupied with problems of individual plant selection as forest tree improvement. It is obvious that clonal and progeny tests are difficult and expensive, impressing the need for highly effective statistical designs. Heritabilities are not yet known for many characters; little assessment has been made of heritabilities with row crops, since they become more or less obvious in large progeny tests. Only with industry's direct participation can forest improvement afford to establish the large populations necessary to permit rapid selection progress; but then industry will be the first to gain by it.

8. THE TREND TOWARD ACCELERATION OF GENERATIONS

Although Hawaii is often described as a "large winter greenhouse," its potentiality as a site for year-round seed production is only beginning to gain recognition (Brewbaker and Hamill, 1967). In our Hawaiian corn breeding, we are disappointed when we fail to get 3 generations per year, and a Hawaiian forester is disappointed when he fails to obtain 15-20 ft. of growth the first year (in species like the tropical ash, Australian toon, or eucalypts). Other tropical areas have been exploited increasingly by plant breeders in the past decade to permit acceleration of breeding programs. This demand has been most insistent for the breeder of annual crops, who often has well-defined objectives that are 6 to 8 generations away (e.g., conversion to a new recessive allele, like o_2).

There are few crops in which breeding objectives and methods are not influenced by accelerations in the seed-to-seed cycle. Methods of grafting, chemical regulation of flowering, and growth in greenhouse have been applied successfully in forest breeding, and perhaps our Hawaiian winter greenhouse will be called upon in the near future. The breeder is well aware of methods to circumvent population-genetic shifts when breeding is conducted out of the region of utilization, and care will be necessary in selecting to avoid too dramatic a shift to early flowering. The potentiality of accelerating genetic gains should encourage all efforts to reduce generation time with forest trees.

9. THE TRENDS IN THE USE OF INDUCED POLYPLOIDS

Breeders are occasionally encouraged by young geneticists to become excited about a hot new technique which promises to revolutionize breeding progress, if only the breeder weren't so stubbornly conservative. Will Rogers used to tell of an eager young county agent who told a farmer, as they leaned over the rail of a pigpen "Do you realize that if you'd boil that corn, the hogs will digest it twice as fast?" The farmer thought about that a minute, then said, "Aw, shucks, that's all right, they ain't in no hurry." Some of the things we learn from modern genetics are about as valuable to the breeder as serving boiled corn to a hog. Nonetheless, we live in an exciting decade in biology (as we are constantly reminded by anyone working on DNA), and the breeder is obliged to ask "what good is all of this?" if only because the molecular biologists aren't likely to ask it themselves.

Several genetic techniques seem to have been been overrated to the breeder and among these are induced polyploidy and induced mutations. The direct advantages of polyploids, in size, have generally been outweighed by their disadvantages; sterility in the case of seed-producing crops, and reduced growth rate in vegetative crops. In either instance, a major problem is the low rate of genetic advance when breeding at the polyploid level.

The elegant work of people like Sears and Riley has indicated that many polyploids are effectively diploidized by genes controlling intergenomic pairing, and the value to the breeder of these in induced polyploids is encouraged; the rarity of polyploidy in gymnosperms might be taken as **a priori** evidence that such genes do not occur there.

The early predictions for polyploids were perhaps overstated by some geneticists, yet there are specific instances of their obvious value even in forestry. For gene transfer, induced tetraploids of **Ulmus pumila** are of interest in relation to breeding of the tetraploid American elm, and the aspen triploids are of immediate interest (although the breeder will probably soon provide diploid hybrids to replace the triploids).

A major accession to the use of polyploids is that they should be better buffered against ecologic challenges, etc., but this may be of particular importance only where clones or inbred lines are in use.

10. TRENDS IN THE USE OF INDUCED MUTATIONS

Induced mutations have, it seems to me, been oversold to the breeder. While touted as a source of new genetic variability, or as a means of obtaining a given genetic trait in an otherwise suitable background, induced mutations simply have not paid for the research investment. This is not to question the insight that they have given, and continue to give, into basic phenomena.

Radiation-induced mutants, in particular, regularly carry associated genetic damage that is undesirable and often impossible to circumvent by breeding. Chemical mutagens, like ethylmethanesulfonate, may ameliorate this problem somewhat. The fact is, of course, that most breeders have more genetic variability at their disposal than they know what to do with. If a new trait is desired, induced mutation is often an unlikely and most expensive method of seeking it.

11. TRENDS IN STATISTICAL GENETICS

While the colchicine breeder may be behind us and the mutation breeder somewhat passe, the computer breeder has only begun to rear his head, and some wild predictions of his contributions will doubtless soon be forthcoming. I must only express admiration for the calm predictions of forest biometricians.

I once told Dr. H. K. Hayes, my chief at the University of Philippines, that I thought I'd better compute some heritability coefficients on a couple of characters in rice before I set up my selection program. Hayes harumphed as only he could do and said, "Now, Brewbaker, you just get off your . . . . and spend two months in the rice field, and you won't need to calculate any coefficients at all."

Breeders with the genius and the trained eye of Dr. Hayes never eschew statistics, but never are wed to it either; one often fears that the population geneticist is simply describing in statistical language what these breeders knew all along. Regrettably, the breeder often hasn't said or published what he knows, for he only feels it or senses it intuitively. While we cannot doubt this intuition, we cannot fail to criticize him for not having found a means of communicating it to others. This stems in part from our unrealistic concern, as applied scientists, that we must communicate in the same scientific-sounding language as that of the basic scientist; certainly the social scientist feels under no such compunction, nor should we. Foresters evidently feel that they communicate about as badly as do other agriculturists; somehow the smooth-tongued orators who always pestered the prof in class end up working at the scope or computer, writing monthly articles to Nature, and getting federal money for research of only vague relevance to applied research problems. Nowhere is this sense of the failure of communication so keen as in the gap between statistical geneticist and the field breeder.

Estimates of heritability and of epistatic variance in heterogeneous forest material illustrate the difficulties of their application as well as one could with any crop. Clearly, heritabilities must be assessed where site variability is minimal, and the immense variation observed between sites is fully predictable. The tree show of clonal material and of selfed or testcross progenies seem much more fruitful in assessing usable genetic variance for selected traits in the long run. I am less impressed now than I would have been a year ago by the need in forest improvement for indices of selection since an initial reaction to forest breeding is that one must work with such small progenies; this is simply not the case. Reviewing the contribution of indices in plant breeding, D. C. Smith (1964) expressed a general disappointment in the application of selective indices for breeding to improve yield. Computer refinements speed calculation, but probably cannot bring sufficient precision for their use except in rare instances. Again this does not militate at all against the contribution of the computer in accelerating the whole process of data retrieval in the breeding program.

The complication of linkage alone has made statistical genetic evaluation of overdominance and epistasis most tenuous even with row crops grown in large populations on extremely uniform sites. This should not disparage such efforts for selected characters in forest trees, but we should not expect a greater impact of these computations in forest breeding than in other crops.

12. TRENDS IN THE APPLICATION OF BIOCHEMICAL AND MOLECULAR GENETICS

The decade just past belongs to the molecular biologist. In its way, it has seemed an era of almost pristine aloofness to the plant breeder's problems, or to problems that cannot be related to the more lucrative ills of **Homo sapiens** or **E. coli.** Biochemical genetics has unraveled much of the mystery of the gene (**sensu** unicellular organisms), but the fact is that most of the studies of DNA, RNA and so forth have been essentially of no relevance to the problems of the plant breeder. Much has been learned also of biosynthetic pathways, and of the positions that sugars and pigments and other substances occupy on chromatograms; these studies seem also to have shed little light on plant breeding progress.

The improvement of assay apparatus, however, has offered exciting opportunities for cooperative biochemical-breeding efforts, in studies of proteins, enzymes, oils, alkaloids, resin constituents, etc., of more immediate value to the breeder. The application of paramagnetic resonance apparatus in selection for increased oil contents is an example; seeds of many species may be assayed for oil content without affecting their viability, promising rapid strides in selection progress. Apart from relating plant chemistry to disease and pest resistance, new techniques may reveal biochemical indicators for graft incompatibility, for epicormic branching tendencies, for heterosis, for sex in dioecious trees, etc. In selecting for heterosis, antigenic heterogeneity has been used by poultry breeders, for example, as indirect evidence of superior combining ability, and we may expect that the level of protein or enzyme polymorphism (i.e., total number of such proteins) might correlate as well with the vigor of a tree's progeny as with the offspring of a rooster or prize bull. We cannot underestimate the important fact that each plant cell is endowed with the tree's entire genotype. The probability must be asserted of stimulating genic (enzymic) expression in seedlings, tissue cultures, etc. normally observed only in mature tissues.

13. A NEW TOOL–GEL ELECTROPHORETIC ANALYSIS OF ISOENZYMES

Having been a little harsh on biochemical genetics in general, it may seem incongruous to conclude with this discussion of the enzymes of plant tissues. However, a new and simple technique has emerged that seems to bring the enzyme into a most significant position in the arsenal of the plant breeder. The majority of my laboratory research is now dedicated to studies using this new technique of gel electrophoresis, and of the enzyme variants called isoenzymes which it reveals in higher plant tissues.

Almost 25 years ago, Beadle and Tatum (1941) drew the remarkably simple but profound conclusion that genes regulated systems in living organisms through their production of enzymes, and that most single genes should be identifiable with single enzymes. To be sure, we can now embellish this statement with much more sophisticated knowledge of DNA, RNA, and proteins. The fact that the

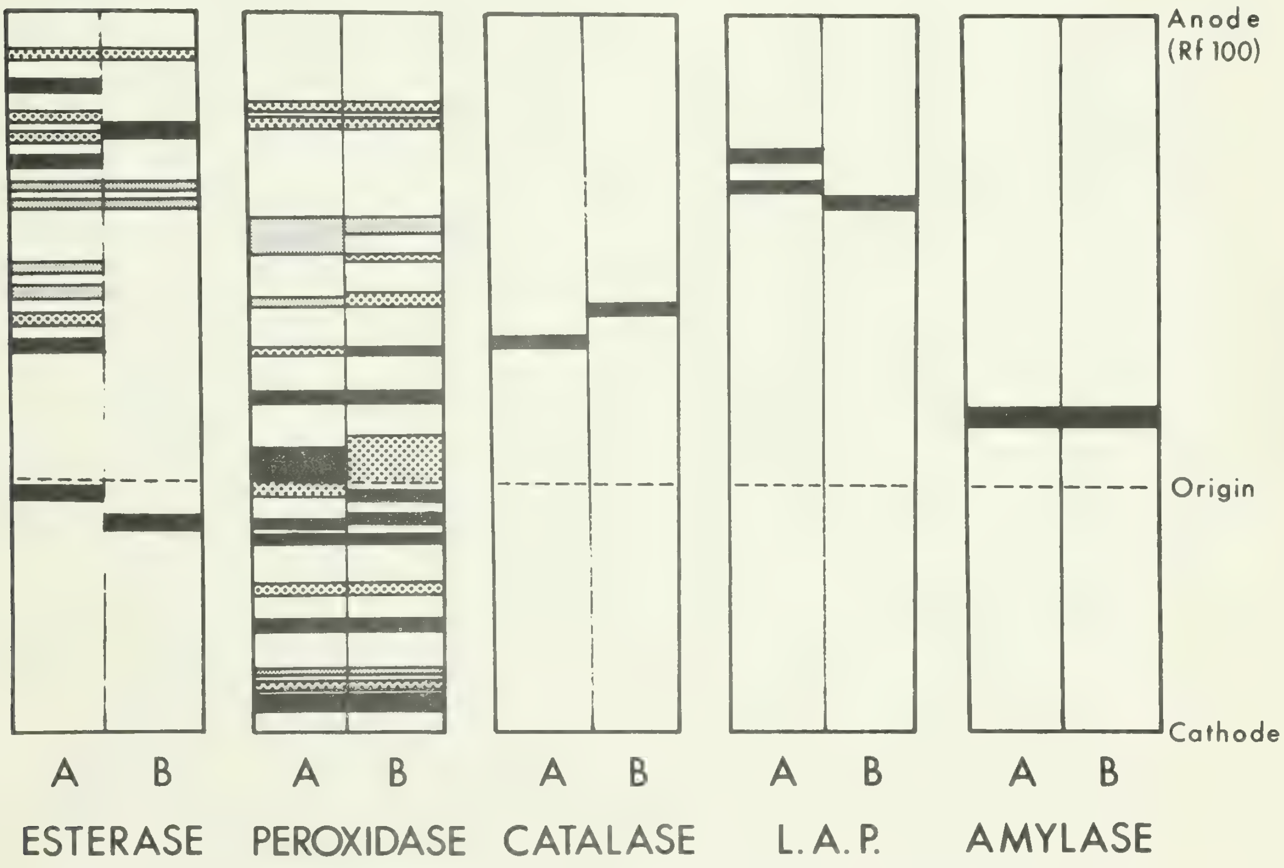

Figure 1 - - Some comparative isoenzymic patterns of two corn inbreds (A = Hawaiian sweet inbred AA9; B = Conn. Sweet inbred C42). Starch gel electrophoresis of macerated seedling root.

action of the gene is mediated initially through an enzyme or protein molecule has drawn focus on methods of locating and studying these molecules. Gel electrophoresis provides such a method.

It has long been known that proteins migrate in electric fields, having a positive or negative charge under appropriate pH conditions. In 1955, Dr. O. Smithies discovered that proteins could be separated most satisfactorily on a gel made of starch which could then be stained for the presence of enzyme bands, a process as inexpensive as it is elegant. We commonly use a starch gel, acrylamide or agar gel about 7" square and ¼" deep. Extraction procedures can be comparatively crude; tissues are often macerated in saline, and a ¼" square piece of filter paper soaked with the macerate. About 20 of these papers are inserted into the gel, and 250V (DC) applied for about 4 hours to the gel, a standard refrigerator accommodating about 8 gels. The gels are removed, slit into 2 or 3 wafers, and stained for enzyme systems of interest.

A major limitation of this system is enforced by the few staining procedures as yet available. Nonetheless, enzymes which may be studied easily are rather important ones, including esterases, peroxidases, amylases, catalases, phosphatases, dehydrogenases, and aminopeptidases (figure 1).

Using the gel technique, we find that even highly purified plant proteins are complexes of many different proteins which can be separated electrophoretically. These separated proteins with the same function are designated isoenzymes by Markert and Moller (1959); they are seen as bands when properly stained on the gel. Purified horseradish peroxidase, for example, contains at least 7 different enzymes, while we find at least 25 different peroxidases from tissues of corn.

Genetic data make it clear that most of these separated isoenzymes are under the control of single gene loci. Some isoenzymes are universally present in tissues of a species, suggesting that they are indispensable; species can occasionally be distinguished by such non-polymorphic loci. Other isoenzymes vary from tissue to tissue or plant to plant, with high activity in some but none in others. Such presence vs. absence patterns are often under the control of "operon" like genes. Many isoenzyme variations prove to be allelic, with alleles at a single locus governing the synthesis of two isoenzymes with slightly different electrophoretic mobility. Generally, hybrids carry the enzymes of both parents in selected instances, as in the catalases of corn, the hybrids show bands which are not present in the parents (Beckman, Scandalios and Brewbaker 1964). The ability to identify hybrids from their parents has obvious applications to plant breeding, apart from its intrinsic relevance to the phenomena of heterosis and homeostasis.

The potential applications of isoenzyme techniques in forest tree research appear fascinating, although no one would predict it to be a panacea for problems. Nonetheless, isoenzymes are excellent genetic markers; an inch of root, ¼" plug of cambium, or pollen from a single cone provide sufficient material to test for perhaps 60 different isoenzymes (=genes?) of those we have studied (fig. 1). Such genetic markers seem ideal for identification of species hybrids, distinguishing selfs from crosses, or stock from scion wood, etc. Their potential use in evaluating combining ability, graft incompatibility, the tendency to traits such as spiral grain and epicormy, etc., offer intriguing opportunities for research. Perhaps electrophoresis will not spawn a generation of isoenzyme breeders, but we may nurture the hope that it will help to repair the gap that has widened between biochemical genetics and the problems and progress of the plant breeder.

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TECHNICAL SESSION

Geographic Variation in Specific Gravity and Three Fiber Characteristics of Sweetgum

JOHN W. JOHNSON and ROBERT L. McELWEE[1]

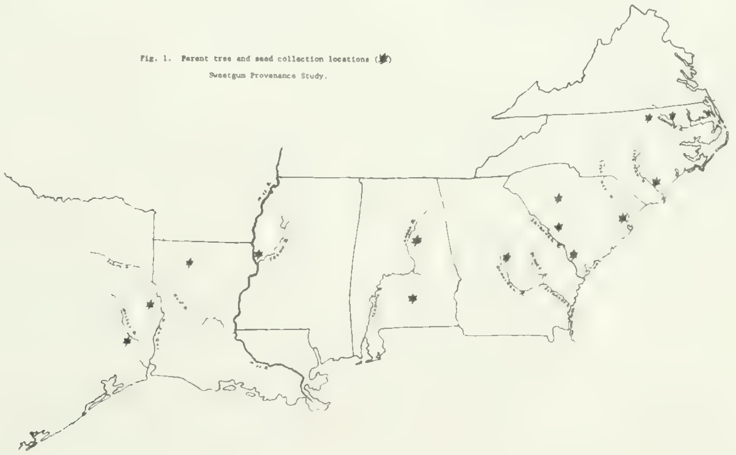
In mid-1964, at the Annual Advisory Committee Meeting of the North Carolina State-Industry Cooperative Hardwood Research Program, participants in the Program endorsed plans for a major seed source study involving sweetgum over that part of its range from northeastern North Carolina to eastern Texas. Such a study has been established. It includes as one of its component parts the use of seed trees whose individuality is described and maintained throughout the life of the study from the the nursery phases of the work through the outplantings and on to final results at some time in the future.

No study of this breadth and complexity is undertaken lightly. Sweetgum, in terms of where and how it grows, its uses, and the quantities consumed, is the most important single hardwood species in the United States. Its uses cover the range of quality aesthetics from fine face veneer through box lumber and dunnage to pulpwood. It grows almost everywhere, though not necessarily well. Furthermore, it appears to be amenable to management and manipulation, both genetically and silviculturally. In short, sweetgum is a tree species and a timber commodity very much worth studying from the standpoint of variation, whatever may be its cause. The investigation reported here covers possible provenencial variations in certain wood characteristics that bear importantly on its utilization.

Sample Collections

It has been mentioned that the N. C. State-Industry Sweetgum Provenance Study extends geographically from North Carolina to Texas. Within this broad region, seven collection transects distributed more or less uniformly over the area were arbitrarily selected. Typically, each transect contained a collection point within a major river drainage in the Coastal Plain and a companion collection point in the Piedmont. One transect, however, consisted of a collection point in the Mississippi River Delta near Vicksburg, Mississippi, and a companion location in the north-central pine uplands of Louisiana, near Hodge. The last transect, in East Texas, consisted of two collection points, one along the Neches and the other near the Sabine River. There is, rather obvidously, little physiographical differentiation between these two points. Figure 1 indicates generally the collection locations for seed and wood samples for the study.

Fig. 1. Parent tree and seed collection locations (★)
Sweetgum Provenance Study.



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Within each collection location, two sweetgum stands were selected on average to good sites for the species and sufficiently distant from each other to eliminate the likelihood of common parentage. Then within each stand, five of the better dominant or codominant trees were selected as sample trees; as with stands, these trees were far enough apart to reduce chances that any two might have originated as sprouts from the same root system. There were, thus, seven transects, two physiographies per transect, two stands per physiographical location, and five trees per stand, or a total of 140 sample trees.

From each of the 140 trees, sufficient fruits were collected to produce seed and seedlings for the necessary outplantings. Two 10 mm. increment cores were extracted from each sample tree at approximately breast height and at points 180° apart on the circumference of the stem. These cores were shipped immediately to Raleigh for specific gravity and fiber characteristics determination.

Sample Measurements

The 10 mm. increment core samples were maintained moist and cold in Raleigh until sectioning, treating, and measuring. Each core was, first, divided into three segments. The first began at the pith and extended through the first ten annual rings; the second began with the eleventh and continued through the twentieth rings; and the third included the rest of the core. Specific gravity was determined for each of these core segments on a green volume-oven dry weight basis, with volume being measured by the water-displacement method. The two determinations for any particular segment were averaged to obtain an expression of specific gravity for that segment.

Following measurements of specific gravity, the fifteenth and thirtieth annual rings of one core from each tree were determined as carefully as possible, excised, and chemically macerated to separate the fibers using Franklin's method (1) Measurements of length to the nearest 0.1 mm. were made on 40 unbroken fibers for each annual ring sample for each core. Measurements of cell wall thickness and total fiber diameter were determined from 10 fibers to the nearest ocular micrometer graduation, with a magnification of 450x. These measurements were then converted to microns.

Analysis of Data

In keeping with the main objectives of the overall study, the principal matters of interest in our wood and fiber characterization work were the variations that exist between trees and between stands in each of the two physiographies, Coastal Plain and Piedmont, on each of the seven transects from North Carolina to Texas. The data, averaged by stand, are shown in Table 1. Sweetgum fibers average about 2 mm. in length, and weighted specific gravity at breast height approaches 0.50, which checks closely with other measurements of these characteristics.

A series of analyses of variance were run for all of the characters measured. Some of these results are presented here.

Specific Gravity Variation: Between-Trees

Variation studies in other species, pine and hardwood, have routinely indicated significant specific gravity differences between trees in a given stand. While there was no reason to suspect anything different from the data collected here, the dual coring of each sample tree enabled an analysis of variance using within-tree gravity variation as the error term. Only the outer-segment data --- from the 21st annual ring on --- were used for the first analysis. Specific gravity of this portion of the core would be more truly representative of tree specific gravity at breast height than would similar information for the other segments. A nested classification was used in the analysis of variance, with cores in trees being used to test trees in stands and stands in provenances; with stands being used to test provenances in transects; and with provenances being used to test transects.

No significant differences at the 5% level were found in outer wood specific gravity between trees (Table 2). This was so unexpected that a second analysis--- this time using the core segment that contained the 11th through the 20th annual rings--- was run. Patterns of significance were exactly as shown in Table 2 for outer wood: there were highly significant differences between stands, but none between trees. We cannot pretend that these results are fully or perfectly indicative; our sample was only five trees per stand, and the analyses were for single, separate segments of each core. The preponderance of data from other studies strongly suggests the existence of significant tree-to-tree differences in specific gravity. Our data do not confirm significant tree-to-tree variation; we recommend additional, more-intensive studies of this characteristic.

Specific Gravity Variation: Between Stands, Provenances, and Transects

After analyzing between-tree variation in specific gravity, as indicated by the outer-wood

Table 1. Averages by stands for specific gravity, fiber length, width, and wall thickness. Sweetgum Prov. Study

Transect Provenance Stand	Sp. G. 1st 10 rings	Sp. G. 2nd 10 rings	Sp. G. outer rings	Sp. G. weighted	Fiber length 15th yr.	Fiber length 30th yr.	Fiber width 15th yr.	Fiber width 30th yr.	Wall thickness 15th yr.	Wall thickness 30th yr.
					----- mm -----		------------ microns ------------			
1-A-1	.514	.522	.496	.496	1.87	1.99	27.94	30.70	7.63	8.91
1-A-2	.476	.500	.494	.494	1.74	1.88	28.30	30.72	7.25	7.87
1-B-1	.512	.520	.512	.513	1.93	1.91	30.11	28.66	7.59	7.97
1-B-2	.474	.486	.484	.484	1.92	2.10	29.39	29.82	7.39	8.09
2-A-1	.490	.510	.518	.515	1.94	2.21	26.39	26.87	7.63	8.09
2-A-2	.448	.474	.488	.486	1.77	1.95	26.64	28.92	7.22	7.92
2-B-1	.470	.482	.494	.491	1.87	2.04	27.28	28.60	6.95	8.07
2-B-2	.488	.476	.476	.476	1.86	1.83	27.98	28.61	7.59	8.72
3-A-1	.506	.534	.536	.533	1.92	2.10	28.56	28.99	8.52	9.16
3-A-2	.464	.474	.470	.470	1.80	2.04	29.20	28.90	7.21	8.02
3-B-1	.436	.484	.490	.488	1.80	1.86	28.55	29.56	7.16	8.62
3-B-2	.502	.518	.512	.513	1.60	1.90	26.16	28.72	6.88	8.19
4-A-1	----	----	----	----	----	----	-----	-----	-----	----
4-A-2	.496	.496	.504	.502	2.03	2.11	28.38	29.35	7.97	8.36
4-B-1	.444	.460	.466	.465	2.02	2.12	26.32	27.99	7.17	7.55
4-B-2	.462	.492	.502	.499	1.87	1.88	25.40	26.92	7.08	8.62
5-A-1	.460	.488	.494	.492	1.75	1.91	29.33	29.28	8.28	8.74
5-A-2	.500	.526	.508	.509	1.81	1.90	26.97	26.78	7.41	8.44
5-B-1	.484	.496	.500	.499	1.67	1.92	26.95	28.71	7.72	8.33
5-B-2	.506	.504	.500	.501	1.75	1.89	27.06	27.41	7.59	7.96
6-A-1	.550	.558	.550	.553	1.66	1.85	25.38	26.47	7.08	7.86
6-A-2	.464	.478	.492	.489	1.93	2.12	27.50	27.53	7.40	7.86
6-B-1	.472	.488	.484	.484	1.89	1.97	26.75	27.85	6.61	6.81
6-B-2	.476	.474	.484	.486	1.65	1.90	26.03	29.04	6.97	7.25
7-A-1	.480	.490	.496	.494	1.68	1.86	26.28	27.86	6.84	7.93
7-A-2	.482	.494	.484	.485	1.76	1.92	25.92	25.44	6.67	6.95
7-B-1	.468	.478	.498	.491	1.79	1.83	24.07	23.82	8.13	7.87
7-B-2	.466	.480	.492	.496	1.70	1.77	22.84	25.86	7.27	8.13

Table 2. Analysis of variance for outer-wood specific gravity at breast height.

Source	df	MS	F
Total	269 [1]		
Transect	6	.00085	.388
Provenances in transects	7	.00219	.584
Stands in provenances in transects	13	.00375	6.048**
Trees in stands	108	.00067	1.081
Error	135	.00062	

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[1] One stand of five trees (ten cores) was inadvertently omitted from the sample. Thus, there are 269 df here rather than 279.

** Significant at the 1% level.

of breast-height samples, data from the two increment cores of each tree were combined. Analyses of average specific gravity were then made in terms of each segment and for weighted specific gravity for the entire tree. Only the analysis for weighted gravity is discussed here.

Again, a nested classification was used, following the order trees in stands in provenances in transects, then stands in provenances in transects, then provenances in transects, and finally transects. The analysis--Table 3--shows significant differences only between stands, but at the 1% level. While the analysis of variance of Table 3 is for weighted specific gravity only, the same pattern occurred for specific gravity of each segment.

Table 3. Analysis of variance for weighted specific gravity at breast-height.

Source	df	MS	F
Total	134		
Transects	6	.000571	.429
Provenances in transects	7	.001330	.567
Stands in provenances in transects	13	.002346	4.546**
Error	108	.000516	

** Significant at the 1% level.

Fiber Characteristics Variation

A slightly modified approach was used in analyzing the differences in fiber length, width, and wall thickness of the wood samples used in the study. These characters were measured for the 15th and 30th annual rings of one core only from each tree. Thus, it was possible to use the within-ring sum of squares as the error term to evaluate differences between annual rings and between trees; thereafter, the nested classification was again used for stands, provenances, and transects.

The pattern of variation discerned from these analyses was not so regular as was that for specific gravity. Fiber width was found to vary significantly by transects at the 5% level. We suspect this to be a quirk of the data, and not really meaningful. Analyses of variance for the fiber characteristics measured are shown in Table 4. Age of wood, or annual ring, proved to be highly significant as a source of variation, as did trees within stands, for all three of the fiber characteristics measured. Variation between stands was significant only in the case of fiber length.

Correlations

As a second step in analyzing the mass of data that had been collected, correlations were run between certain of the characteristics. The objective here was to shed light on the predictability of a character from another character easier to measure or measurable at an earlier age; and to indicate limitations or lack of limitations in selections and breeding for specific wood or fiber characteristics. The correlations should not be

Table 4. Analyses of variance for fiber length, fiber width, and wall thickness.

		Fiber length		Fiber width		Wall thickness	
Source	df	MS	F	MS	F	MS	F
Total	269						
Transects	6	0.1839	2.404	68.248	4.644*	3.284	1.431
Provenances	7	0.0765	0.825	14.697	2.361	2.295	1.538
Stands	13	0.0927	4.233**	6.225	1.419	1.492	1.654
Trees	108	0.0219	1.991**	4.388	1.779**	0.902	2.775**
Annual Rings	1	1.3174	119.7**	70.994	28.789**	33.715	103.738**
Error	134	0.0110		2.466		0.325	

***Significant at 1% level.*
**Significant at 5% level.*

construed as indicating cause and effect.

The correlations that were calculated are as shown in the following listing of characters and r-values:

1. **Specific gravity 0-10 yr. to weighted**	r = .662*
2. **Specific gravity outer wood to 30th yr. fiber length**	r = .290
3. **Fiber length 15th yr. to 30th yr.**	r = .766
4. **Fiber length to fiber diameter, 30th yr.**	r = .475*

(*Significant at the 1% level).

Other correlations are available from the basic data. Those shown, however, appear to be the most meaningful in terms of the specified objectives.

DISCUSSION

We are surprised that differences in outer-wood specific gravity prove to be of no statistical significance in light of between-tree variations shown by Webb (6) for sweetgum, by McElwee and Faircloth (3) for tupelo, by Taylor (4), Thorbjornsen (5), and Kellison (2) for yellow-poplar. We suspect this to be a function of the relatively small number of trees per stand that made up the sample. The mass of published data that show significant between-tree differences in wood specific gravity for sweetgum and other hardwoods appears to outweigh the data presented here. The discrepancy between our results and those of other investigators calls for additional definitive investigations.

Lack of significance for specific gravity differences between provenances and between transects is not so perplexing as the non-significance of between-tree differences. The only significant gravity differences were between stands. Analyses of outer-wood specific gravity (Table 2) and weighted specific gravity (Table 3) show the same significance or lack of it for the possible sources of variation.

The highly significant differences in fiber length that show up between the 15th and the 30th annual rings concur with previous reports. In almost every case the outer ring has the longer fiber, which could bear importantly on pulpwood rotation ages. It is gratifying that significant differences exist between trees, particularly since fiber length increases will almost certainly be an important objective in improvement programs. The between-stand differences should not be ignored; they will be of considerable practical importance in tree selections. You will recall Squillace's strong recommendation at this conference that mass selections be made within the best stands on a given site. Within these best stands, individual tree selections will take advantage of the between-tree variation that was found in the fiber length characteristic.

No such complexity exists in the analyses of fiber widths and cell wall thicknesses. Only those differences between rings and between trees were significant.

The correlations noted previously reveal interesting possibilities for predictions of wood and fiber characteristics from measurements made relatively early in the life of a sweetgum. For example, weighted breast-height specific gravity of merchantable trees can be determined quite closely from specific gravity of ten-year-old saplings, and fiber length of the 15th annual ring is a strong indicator of fiber length of the 30th ring. Equally interesting and useful are the indications that specific gravity and fiber length of the outer wood are weakly related at best, as are fiber length and fiber diameter at the 30th annual ring. These characteristics, each potentially important in tree improvement programs, are independent of each other. Selections and breeding for specified degrees of one need not result in degradation of quality in the other.

Of most immediate interest and value, however, is the repeated assurance of these data that differences in wood and fiber characteristics over major changes in geography--North Carolina to Texas and Coastal Plain to Piedmont are not statistically significant, and need not, therefore, complicate selection and breeding programs. Other phases of the basic study will reveal in years to come the possible existence and importance of provenances in sweetgum growth and development.

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Self-Incompatibility in Sycamore

J. W. BELAND[1] and LEROY JONES[2]

ABSTRACT

Much of the reputed low germination from American sycamore may be due to self-incompatibility or lack of pollen from other trees. Germination tests and X-ray analysis revealed 30-80 percent normal germination from polymix pollinated seed. Only 0-2 percent of the seed resulting from self-pollination germinated normally. No viable seed was obtained from isolated, unpollinated flowers.

Interest is increasing rapidly in improvement and utilization of American sycamore (**Platanus occidentalis L.**). It is valuable for veneer, lumber, and pulp, and susceptible to only a few diseases. Sycamore grows fast throughout its life and attains a larger diameter than any other American hardwood (Betts 1945); within its range, only cottonwood and sometimes a few of the pines produce more volume per acre.

This paper reports the initial results of studies to: (1) determine the feasibility of control-pollinating sycamore, (2) assess the self-and cross-fertility of the species, and (3) determine the receptive period of the flowers.

METHODS

Four sycamore trees in south Mississippi were selected because they were easily accessible and most of them flowered abundantly. Trees 1 and 2 were approximately one-half mile apart. Trees 3 and 4 grew close together.

Female flower heads on each tree were covered with viscose bags as soon as the heads began to break the bud scales. The bagging was done during the third week in March 1966. Male heads were collected from each tree at the time of bagging, and pollen was taken from them with a warm-air extractor, after which it was refrigerated until use a few days later. One hundred normal heads yielded about 8 cc. of pollen. At anthesis, controlled-pollinations were made as follows: (1) self, (2) each tree by every other tree, and (3) three trees by a polymix of the four trees. Tree 2 bore only enough flowers to allow controlled pollinations by self and each of the other trees, and not enough for polymix pollinations. Several flower heads on each tree were bagged but not pollinated.

On tree 1, polymix pollen was applied by hypodermic syringe as soon as the flowers appeared receptive and 1, 3, 5, 7, 12, 16, and 18 days thereafter. Anthesis occurred 5 days after the flowers appeared receptive.

The bags remained over the flowers for 1 month to assure adequate isolation from contaminating pollen.

The seed was collected in November 1966 and crosses kept separate. Because an unknown number of seed was lost during cleaning with a sieve, no estimate of viable seeds per pollination was attempted.

The U. S. Forest Service's Eastern Tree Seed Laboratory at Macon, Georgia, tested germination. The design was a randomized complete block, with 5 replications and 100 seeds per sample. An arcsin transformation and analysis of variance were conducted on the germination data. Differences between means were evaluated by Duncan's test (1955). Each 100-seed sample was examined by X-ray prior to the germination test as a means of predicting germinability from the internal structure. The seeds were arrayed for all testing on a 10 by 10 grid, making X-ray prediction and data of actual germination for each seed easy to compare.

RESULTS

Sycamore appears to be highly self-incompatible. Average germination from selfing ranged from 0.2 to 1.2 percent (table 1, fig. 1). There were no significant differences (at the 95-percent level of confidence) among selfed individuals; however, the selfs had significantly lower germination than all

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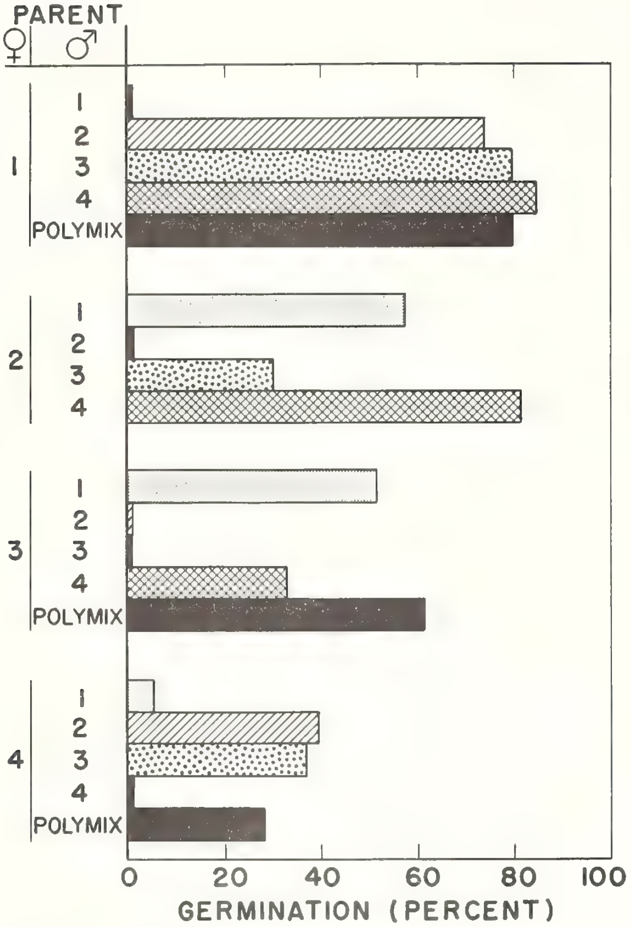

FIGURE 1. Mean germination of control-pollinated sycamore.

other crosses except 3 by 2. The low germinations for 3 by 2 (0.3 percent) and its reciprocal 2 by 3 (15.3 percent) indicate poor crossability between these two trees. Germination was low for 4 by 1 (5.6 percent), probably because of late pollination.

The female flowers were receptive for more than 2 weeks. Pollinations during this period resulted in seed with germinations of better than 50 percent (fig. 2).

No viable seed were obtained from isolated, unpollinated flowers, and X-ray examination revealed no embryos or abortive embryos. Hence apomixis probably does not occur in this species.

Specific combining ability varied widely. Seed from tree 1 gave the best overall germination, and X-ray examination showed it to have more large embryos than seed from trees 2, 3, or 4.

Polymix crosses resulted in germinations rang-

TABLE 1.--MEAN GERMINATION OF CONTROL-POLLINATED SYCAMORE SEED. SIGNIFICANT DIFFERENCES AMONG MEANS ARE INDICATED BY DUNCAN'S TEST (1955)

PARENT		MEAN GERMINATION
FEMALE	MALE	
1	4	84.6
2	4	81.2
1	POLYMIX	79.9
1	3	79.6
1	2	73.8
3	POLYMIX	61.8
2	1	57.6
3	1	51.6
4	2	39.5
4	3	38.0
3	4	33.0
4	POLYMIX	28.1
2	3	15.3
4	1	5.6
2	SELF	1.2
4	SELF	.6
1	SELF	.5
3	2	.3
3	SELF	.2

MEANS REPRESENTED BY THE SAME LINE ARE NOT SIGNIFICANTLY DIFFERENT AT THE 95 PERCENT LEVEL OF CONFIDENCE.

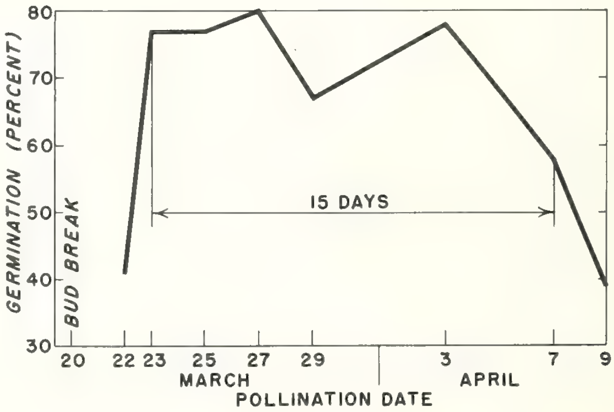

FIGURE 2. Duration of receptivity for sycamore flowers.

ing from 28 to 80 percent (table 1, fig. 1). While there is a greater variation in specific crosses than in polymix crosses, both indicate that sycamore can be efficiently control-pollinated.

Germination predicted from X-ray examination was highly correlated (r=0.99) with germination.

DISCUSSION

The U. S. Forest Service's **Woody-Plant Seed Manual** (1948), summarizing results from 15 lots of seed, reported that germinative capacity of sycamore ranges from 5 to 69 percent, with an average of 35 percent. Germination percentages determined at the Eastern Tree Seed Laboratory usually have been below this average, and have given sycamore the reputation of being a poor seed producer. The study reported here indicates that low germination may often result from self-incompatibility. Trees that are growing singly or that occur as scattered individuals in a mixed stand may not receive adequate pollen from other trees. Much selfing will thus occur, and the seed can be expected to have a low germinative capacity. Boyce and Kaeiser (1961) also found selfing prevented good seed germination in yellow-poplar.

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Seedlings of Two Liquidamber Species Compared

JAMES R. WILCOX[1]

Abstract. In a nursery in southern Mississippi, **Liquidambar formosana** Hance. and sweetgum (**L. styraciflua L.**) seedlings grew equally well in height and diameter for 2 years. The sweetgum had more branches per seedling, and stopped growing earlier in the year; **L. formosana's** wood had higher specific gravity and longer fibers.

Liquidambar formosana is a valuable tree in its range in southeastern China and Taiwan. Trees in natural stands reach a height of 130 feet, and the wood is used in fine furniture. In plantations, trees are typically branchy and poorly formed. In the present study, the early performance of **L. formosana** was compared with that of **L. styraciflua**, the only member of the genus indigenous to the United States. The study was conducted in southern Mississippi where climate is similar to that in **L. formosana's** natural range.

Methods

In the spring of 1964, 4-foot rows in a nursery on the Harrison Experimental Forest were planted with seeds from 42 **L. formosana** trees in Taiwan and four local **L. styraciflua** trees. Immediately after the seedlings emerged, they were thinned to four per foot, approximately equally spaced. Each row contained progeny from one source, and rows were replicated four times.

At the end of the first growing season, date of bud set, total height, diameter at the root collar, and number of branches per seedling were recorded for the five tallest plants in each row. Ranges and variances were computed for plot means. For testing of differences, a confidence level of 5 percent was set.

In the winter of 1964, 103 seedlings of each species were transplanted at the nursery to a 12- by 12-inch spacing. In November 1965, a section 65mm. long was cut from the base of the stem of each of these seedlings. Diameter, specific gravity by the green-volume: dry-weight method, and average length of 60 fibers were measured for each section.

To compare field growth, the remaining seedlings were lifted at the end of the first growing season and outplanted at an 8- by 8-foot spacing in southern Mississippi, and at a 10- by 10-foot spacing in northwestern Mississippi.

Results and Discussion

At the end of the first growing season, morphological differences between species were apparent. Most **L. formosana** leaves had three lobes, some had five; most **L. styraciflua** leaves had five lobes, some had seven. In contrast to sweetgum, the exotic had pubescent stems and branches, and longer and more slender stipules. It did not have corky ridges on stems.

Height and diameter by species did not differ significantly (Table 1). **L. styraciflua** seedlings had more branches and set their terminal buds earlier than **L. formosana** seedlings. Differences among progeny means within species were significant for all the characters just mentioned except number of branches in **L. formosana.**

At the end of the second growing season, both in the nursery and field plantings, differences between species in height and diameter were still insignificant. However, **L. formosana** wood had higher specific gravity and longer fibers than **L. styraciflua.** Thus, although growth was comparable, **L. formosana** seedlings were producing more wood substance. If this trend continues, the exotic species may be a source of germplasm for increasing the specific gravity of sweetgum wood.

In **L. styraciflua**, there was a significant correlation between diameter and both specific gravity and fiber length. Seedlings of larger-than-average diameter tended to have longer fibers and heavier wood than seedlings of smaller-than-average diameter. The same was not true in **L. formosana** seedlings.

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In the widely spaced field plantings, the exotic seedlings branched more than the native sweetgum. This was a reversal of the trend that appeared in the nursery. In form development, it appears that **L. formosana** is more sensitive to competition than **L. styraciflua.**

TABLE 1. Seedling characters by species

CHARACTER	L. formosana			L. styraciflua		
	Mean	Range		Mean	Range	
Plant height (cm.)	62.7	53.1	– 72.6	65.2	59.3	– 69.5
Stem diameter (mm.)	5.8	5.0	– 6.6	6.2	6.1	– 6.4
Number of branches	2.3	0.5	– 4.6	7.3	4.6	– 10.2
Date of bud set	11/20	11/2	– 12/6	10/26	10/16	– 11/3
Specific gravity	.515	.462	– .566	.443	.394	– .490
Fiber length (mm.)	1.28	1.14	– 1.48	1.16	1.00	– 1.30

Physiographic Seed Source Variation in Tupelo Gums Grown in Various Water Regimes

DONAL D. HOOK and JACK STUBBS[1]

Abstract.---One-year-old swamp tupelo and water tupelo seedlings were grown for one growing season in six artificially imposed water regimes with replications in two consecutive years. Height growth, leaf dry weight, total dry weight, stem form A (in flood zone), and stem form B (above flood zone) were measured. Results showed that height growth and dry weight varied significantly between some seed sources for each species. Both height growth and dry weight were lower in intermittent and continuous flooded treatments than under continuous surface saturated treatments. With the exception of one seed source from each species, dry weight production was less in the intermittent flooding than continuous flooding treatment. Stem form (butt swell) appeared to be related more to the presence of flooding than to seed source.

Physiographic characteristics of different types of swamps may impose rigid limitations on seed selection for tupelo regeneration. Swamps that differ in such characteristics as soil origin, water origin, degree of flooding, and type of flooding frequently occur in a relatively small locale in the coastal plain. Consequently, the possibility of seed source variation in tupelo gums is greatly increased in local areas. First year germination and height growth of tupelo seedlings vary significantly between various physiographic seed sources when grown in the nursery bed environment.

This paper reports on a test of variation in growth and morphology of swamp tupelo, **Nyssa sylvatica** var. **biflora** (Walt.) Sarg.; and water tupelo, **N. aquatica** L., from different physiographic seed sources when grown in various water regimes.

METHODS

The study was carried out in the hydroedaphytron at the Santee Experimental Forest, Berkeley County, S.C. This facility was designed primarily for study of wetland problems, consequently control of water and soil is its main and most flexible asset. The structure consists of six growing compartments (6 x 6 x 6 feet) and their flood tanks, which abut each compartment on the north and south sides and allow for water flow from left to right (fig. 1). We can control water flow and level at any depth in the soil by perforated holes in the walls adjacent to flood tanks. Water can be moved over the soil and through the soil

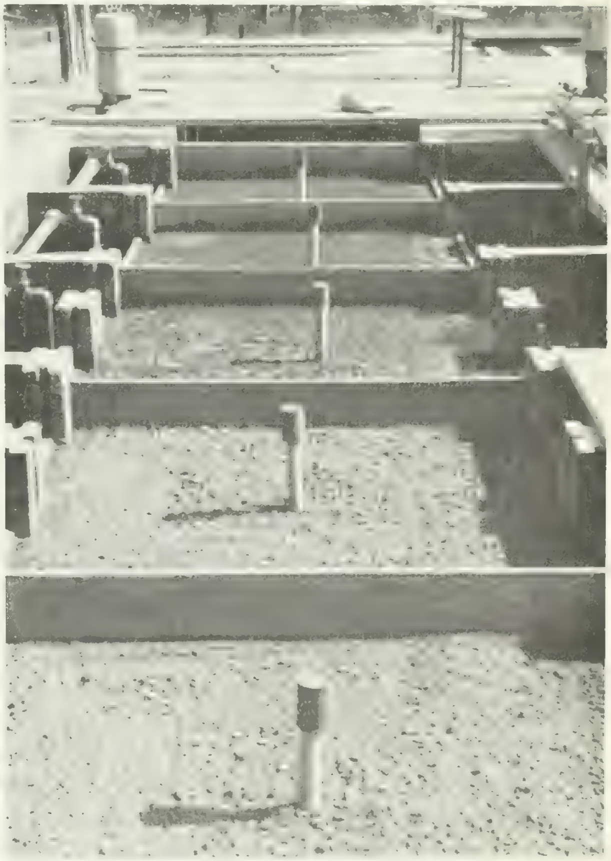

FIGURE 1. An end view of five of the growing compartments of the hydro-edaphytron just prior to planting seedlings in 1965. Flood tanks abut each compartment on the left and right side.

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both horizontally and vertically by controlling the side drain and central drain in each compartment. Water is circulated through the system by either of two pumps. A large pump (2400 gal./min. capacity) is used for rapid water flow and a smaller pump (250 gal./min. capacity) for slow flow rates. Water is obtained from a deep well and is stored in a large central storage tank. The same water is recirculated through the treatments to lessen salt accumulation in the soil.

Species were randomly positioned to either the east or west side of each compartment (fig. 2). For each species, two 1-year-old seedlings from three physiographic seed sources were randomly placed in each row and column of a 6 x 6 Latin square. Each compartment had two Latin squares and each seedling had a 6 x 12 inch growing space.

Selection of seed source was based on preliminary analysis of nursery observations. The seed sources were:

WATER TUPELO

- (RR) Red River Source
    - (1) Santee River
    - (2) Pee Dee River
- (BR) Black River Source
    - (1) Edisto River
    - (2) Black River
- (NA) Non-Alluvial Swamp Source
    - (1) Little Wambaw Swamp
    - (2) Watson Hill Swamp

SWAMP TUPELO

- (BR) Black River Source
    - (1) Edisto River
    - (2) Black River
- (NA) Non-Alluvial Swamp Source
    - (1) Ravenwood
    - (2) Little Wambaw
- (P) Pond Source
    - (1) Jacksonboro-Cottageville
    - (2) Strawberry Rd.

Treatments were designed so that we could compare differences in plant response under continuously flooded, intermittently flooded, and continuously surface-saturated treatments of both stagnant and moving water.

Treatments

I. Surface saturated continuously
  - A. Moving water
  - B. Stagnant water

II. Surface saturated 2 weeks, flooded 8 inches deep, one week, cyclic
  - A. Moving water
  - B. Stagnant water

III. Flooded continuously, 8 inches deep
  - A. Moving water
  - B. Stagnant water

The treatments were started in late April 1964 on the first replication and in early March 1965 on the second replication. They were both stopped in October of the respective years, and seedlings were harvested for measurements.

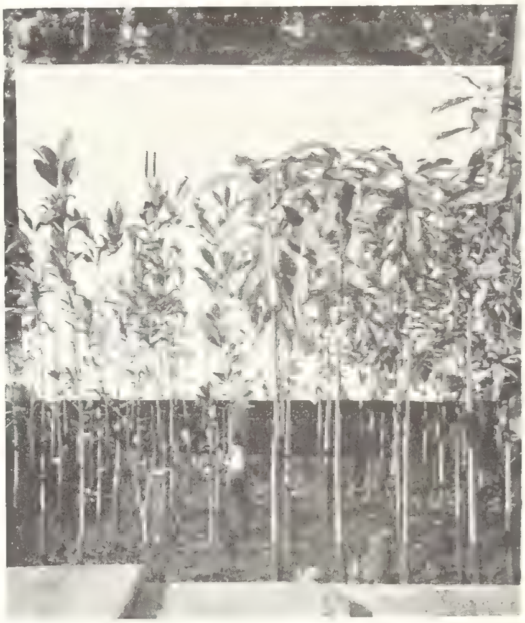

FIGURE 2. Swamp tupelo (left) and water tupelo (right) seedlings in continuously flooded treatment in September 1965. Water was lowered to surface to illustrate seedling position and facilitate photographing.

The soil used was Lynchburg loamy fine sand, premixed and uniformly placed to a depth of 5 feet in each soil tank.

Height growth was measured periodically throughout the growing season for both years. In 1965, we estimated dry weight gain by correlations between fresh weight and oven dry weight at planting and harvesting time. Correlations varied from r= 0.96 to r= 0.99. Leaves were collected each each year in early October and oven dry weight was measured. At harvest time, stem diameter was measured to the nearest 1/100 inch by calipers at 1/4, 6, and 9 inches above the ground line. Diameter at 1/4 inch was divided into diameter at 6 inches to give stem form in flood zone (stem form A), and diameter at 1/4 inch was divided into diameter at 9 inches to give stem form above flood zone (stem form B).

ANALYSIS

Each year's data and the combined two years' data were analyzed separately for each species by the Latin Square Analysis of Variance. Means for within seed source, between seed source, and seed source-treatment interaction were tested for significance by Duncan's Multiple Range Test.

The dependent variables tested for each species were initial height, height growth for season, leaf dry weight, total dry weight (less leaves), stem form A and stem form B.

RESULTS AND DISCUSSION

There were only a few significant within-and between-seed source variations when summed across treatment; however, there were numerous seed source-treatment interactions.

Water Tupelo

Height of seedlings immediately after planting showed significant within-and between-seed source variation. Seed source NA was significantly taller than seed source RR and BR, and seed sources BR and NA had significant within-source variation. The dependent variables of height growth, leaf dry weight, increase in total dry weight, stem form A, and stem form B showed no consistent within-or between-seed source variation when summed across treatments.

The major interactions for water tupelo occurred in moving-water treatments. Growth was consistently better in continuous surface-saturated treatments for all seed sources and decreased with flooding; however, seed source NA did relatively better in dry weight production under intermittent flooding than did seed sources BR and RR. This trend was observed in leaf dry weight (combined analysis) and 1965 total dry weight (less leaves), but was essentially reversed in height growth (fig. 3). The reversal in height growth and dry weight response appears to be related to differences in diameter of seedlings for the different seed sources. Stem diameter at 1/4, 6, and 9 inches above ground (1965) responded the same for seed sources as total dry weight (fig. 3); that is, stem diameter at each position was larger for seed source NA in the intermittent treatment than for seed sources BR and RR.

Swamp tupelo

In 1965, seed source BR for swamp tupelo was lost due to insufficient seed. This reduced the sensitivity of our overall analysis by about one-half. Initial height of seedlings immediately after planting showed no seed source variation in the combined analysis and the separate 1965 analysis. In 1964, seed source NA was significantly taller than seed sources BR and P.

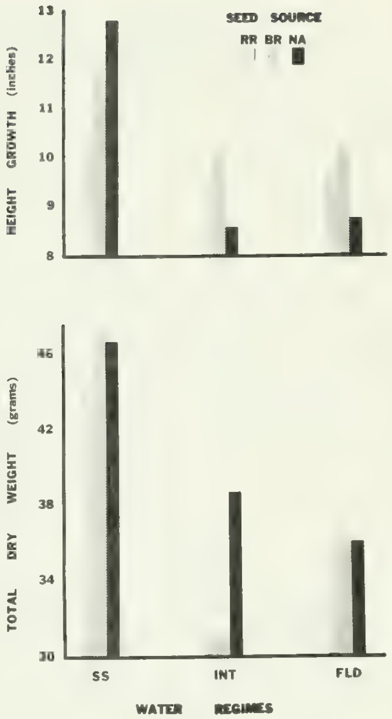

FIGURE 3. Interactions of the three water tupelo seed sources in height growth and 1965 total dry weight (less leaves) with three moving-water treatment regimes: surface saturated (SS), intermittent flooding (Int.), and flooded continuously (Fld.).

Height growth (combined analysis) of seed source NA was influenced more by the intermittent flooding treatment than seed source P (fig. 4). Leaf dry weight (combined analysis) showed no significant interactions with treatments, but increase in total dry weight (less leaves) in 1965 did show a significant interaction. Figure 4 also illustrates the reversed effect of intermittent flooding under stagnant conditions on height growth. The beneficial influence of the intermittent treatment under stagnant conditions can probably be attributed to flushing of toxic compounds from the soil and possibly to improved aeration.

Stem form showed only one instance of seed source variation in the combined analysis. Seed source NA had essentially the same stem form A in moving surface-saturated and intermittently flooded treatments as contrasted to a near linear increase in stem form A for seed source P (fig. 4). Stem form A reflects butt swell, which is so characteristic of tupelo gums. Implications are that degree of butt swell is related more to presence of water, either stagnant or moving, than to seed source.

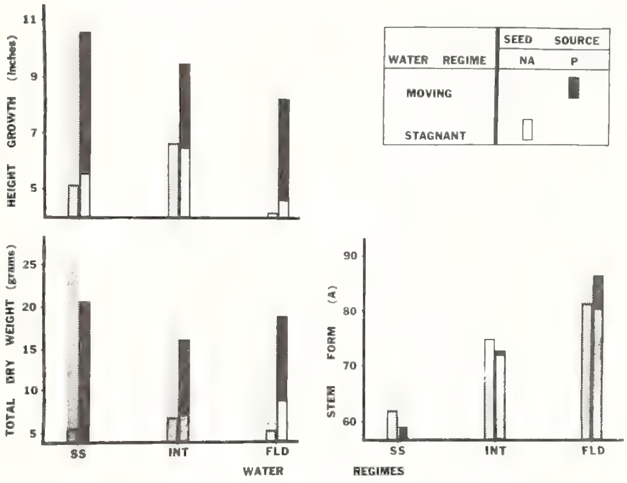

FIGURE 4. Height growth, total dry weight and stem form A for swamp tupelo under moving and stagnant water regimes.

Increase in degree of flooding generally caused a negative effect in growth responses, but intermittent flooding was more detrimental than continuous flooding. Exceptions were seed source NA for water tupelo and seed source P for swamp tupelo--growth of these seed sources decreased nearly linearly with degree of flooding.

Why would intermittent flooding be more detrimental to growth than continuous flooding? One explanation may be found in the adaptative qualities of these species to wetland sites. Both species develop prolific lenticels and water roots under continuous flooding (fig. 5) as contrasted to intermittent flooding (fig. 6). Gas exchange through lenticels is probably beneficial to root respiration under prolonged flooding. The role of water roots is not clear. Intermittent flooding treatments probably cause initiation of water roots and lenticel proliferation during the flooded period, and these new succulent organs were probably damaged by desiccation during the non-flooded period. This suggests that there may be a difference in development and tolerance of the adaptative qualities between seed sources.

Our observations indicate that swamp tupelo and water tupelo seedlings do exhibit physiographic seed source variation under artificially imposed water regimes. How well these data apply to natural conditions is a moot question. We recommend that selections of seed for tupelo gum regeneration be made within physiographic swamp sites and not between such sites.

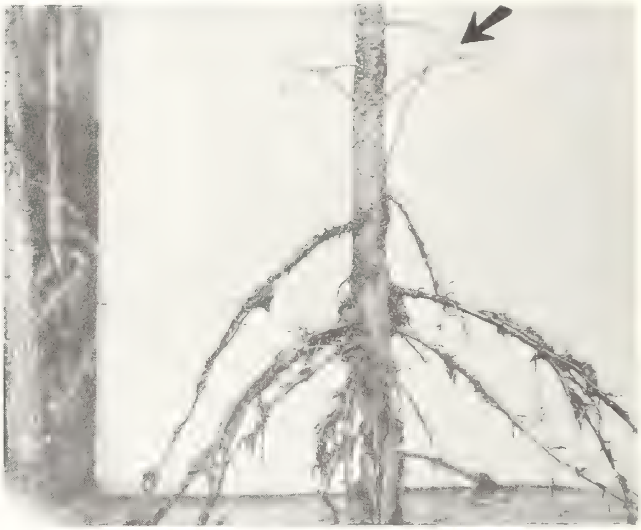

FIGURE 5. Lenticel and water-root development on the flooded portion of a swamp tupelo stem that was flooded continuously by moving water for one growing season.

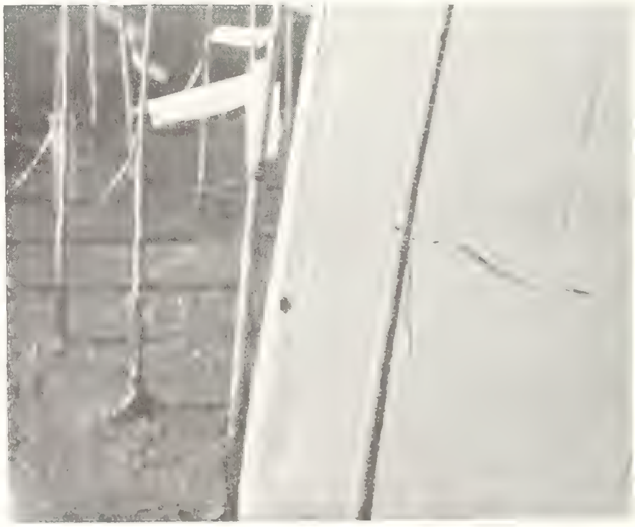

FIGURE 6. Lenticel development on a swamp tupelo stem that was intermittently flooded with moving water for one growing season.

Sixth-Year Results from a Yellow-Poplar Provenance Test

R. E. FARMER, JR., T. E. RUSSELL, and R. M. KRINARD[1]

Yellow-poplar (**Liriodendron tulipifera** L.), one of the South's most widely planted hardwoods, is the subject of intensive research in management and genetic improvement. The association of genetic variation with geographical source is important to both breeding and cultural efforts. Some reported data on racial variation in yellow-poplar fall within a pattern now generally predictable for wide-ranging woody species: Frost damage to material planted in the Midwest is greater in stock from southern than from nothern sources (Funk 1958) and frost damage limits major northward movement of planting stock. This relationship hinges upon genetic variation in photoperiodic response (Vaartaja 1964).

In an Ohio study of racial variation in first-year growth, plants from southern sources were among the largest (Limstrom and Finn 1956). Lotti (1955) observed that 3-year-old Coastal Plain yellow-poplar was taller than yellow-poplar from western North Carolina when both were planted in a small unreplicated test near Charleston, South Carolina. On the other hand, in two replicates of 16 sources (Mississippi to Michigan) planted in western North Carolina, Sluder (1960) found no statistically significant racial differences in 5-year height. Variation in dates of bud-break and growth cessation followed expected patterns, however, with trees from northern sources beginning growth later and ending it earlier than those from southern provenances.

In our study, juvenile growth of yellow-poplar from Coastal Plain and Cumberland Plateau sources has been observed in four plantings near seed origins.

METHODS

Material

In the fall of 1959, seed was collected from four sources:

(1) 10 trees on the University of the South Forest, Sewanee, Tennessee (lat. 35°30', elevation 1,500-1,800 ft.)
(2) 9 trees on the Tallahatchie Experimental Forest, Oxford, Mississippi (lat. 34°30', elevation 200-400 ft.)
(3) 20 trees on the Flat Top Experimental Forest, Birmingham, Alabama (lat. 33°30', elevation 400-600 ft.)
(4) 20 trees on the Homochitto National Forest, Gloster, Mississippi (lat. 31°30', elevation 100-200 ft.)

Trees had average to good form and growth and represented several stands in each of the general collection areas.

Bulked seed from each source was shipped to Stoneville, Mississippi, where it was stratified from late November until late March 1960. Seed from the four provenances was then shipped to cooperators who grew seedlings for their respective plantings. Seedlings for two plantings near Sewanee, Tennessee, were grown at the TVA nursery, Clinton, Tennessee. Material for plantings near Birmingham, Alabama, and Vicksburg, Mississippi, was grown near planting sites.

Planting Sites

At Sewanee, seedlings from the four provenances were planted on a plateau and a cove site on the University of the South Forest. The plateau-top site (elevation 1,850 ft.) lies on a 4-percent east slope and is characterized by a uniform Hartsells fine sandy loam; depth to bedrock is 36 to 48 inches. The cove installation (elevation 1,540 to 1,620 ft.) is on a northwest-facing site with an overall slope of 40 percent; plots are on benches with slopes of 5 to 15 percent. The soil is a Jefferson bouldery colluvium derived primarily from sandstone. Depth to bedrock is extremely variable but averages 20 feet or more. Site preparation on both of these areas consisted of chemically killing all hardwood trees and brush.

The test is replicated near Birmingham in small upland hollows (elevation 490-560 ft.) on the Flat Top Experimental Forest. Soils on the plots are Montevallo or Muskingum silt loams ranging from 2 to 4 feet in depth; slopes are moderate. The planting areas were cleared of a mixed stand of pine and hardwoods, and hardwood stumps were treated with silvicide to prevent sprouting.

The planting at Vicksburg is in a gently sloping field (elevation 200 ft.) adjacent to a moderate-sized intermittent creek. The soil is deep Adler silt loam. The site was disced in preparation for planting.

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[1] Southern Forest Experiment Station, Forest Service, U. S. Department of Agriculture. Farmer and Krinard are stationed at the Southern Hardwoods Laboratory, maintained at Stoneville, Mississippi by the Southern Forest Experiment Station in cooperation with the Mississippi Agricultural Experiment Station and the Southern Hardwood Forest Research Group. Russell is stationed at the Sewanee Silviculture Laboratory, maintained at Sewanee, Tennessee, by the Southern Forest Experiment Station in cooperation with the University of the South.

Climatic conditions in three planting areas are tabulated below. No data are available for the Sewanee cove area.

Planting localities	Mean number frost-free days	Temperatures, °F January average	Temperatures, °F July average	Annual rainfall, inches
Sewanee (Plateau)	201	39	75	56
Birmingham	241	46	80	54
Vicksburg	252	50	81	49

Design and Establishment

Seedlings (1-0) were bar-planted during the winter of 1961 in randomized block designs with four replications at all four locations. Each plot contained 121 seedlings at 5- by 5-foot spacing. Blocks were planted contiguously on the Sewanee plateau and Vicksburg sites. On the Sewanee cove and Birmingham sites, uneven topography necessitated separating blocks by distances of up to ½ mile.

Maintenance and Observations

Weeds in the Vicksburg planting were mowed four times during the first growing season and twice during the second. Competitive growth at the other three sites was not cut. Height and survival after 3 and 6 years' growth were recorded for a central square of 49 trees in each plot. In 1966, foliation dates of 5 trees per plot were observed at Vicksburg and of 2 trees per plot in both Sewanee installations. Foliation of four trees per plot was observed in 1967 at Vicksburg and in the Sewanee plateau planting. Foliation date was defined as the first date on which one or more leaves were completely out of buds, and was recorded as number of days after February 28.

Analysis of variance in all characters took the form of a split-plot design with planting locations as major plots and provenance as subplots. Plot means were the units of analysis.

RESULTS

Survival

Mean 3-year survival of seedlings from provenances represented in the four plantings varied from 75 to 97 percent (Table 1). Survival was lowest (77 percent) at Birmingham and highest (96 percent) on the Sewanee plateau site. In the Sewanee cove planting, trees from the Sewanee source survived less well than those from the Oxford source (.05 level of significance); source differences were nonsignificant at other locations. Increase in mortality between 3 and 6 years was 3.6 percent points on the Sewanee cove site and less than 1 percent in the other plantings. No evidence of cold damage to stems has been observed in any of the plantings, although apices of Gloster seedlings grown at Clinton, Tennessee, were killed by frost in the nursery. Late spring frosts have occasionally caused slight leaf damage in Sewanee plantings.

Table 1. Survival at 3 years of yellow-poplar from four provenances growing at four locations

Provenance	Vicksburg	Sewanee cove	Sewanee plateau	Birmingham
	- - - - - - - - - -	Percent	- - - - - - - - - -	
Sewanee, Tenn	87	83	93	82
Oxford, Miss.	93	95	97	75
Birmingham, Ala.	87	90	96	78
Gloster, Miss.	91	91	96	75
Mean	90	90	96	77

Growth

Mean 6-year heights for the Vicksburg and Sewanee cove plantings were both 21 feet, and heights at Birmingham and Sewanee plateau locations were approximately one-half that (Table 2). Three-year heights followed a similar pattern. These differences in growth on the two groups of sites (Vicksburg and Sewanee cove; Birmingham and Sewanee plateau) were statistically significant (.05 level) for 3- and 6-year heights and the 3- to 6-year height increment.

Source means based on combined data from all four plantings were practically identical. However, comparison of means within locations revealed the following significant differences (.05 level) in 6-year heights:

Gloster > Birmingham at Vicksburg

Oxford > Sewanee at Sewanee cove

Birmingham > Oxford at Sewanee plateau

Trends leading to these differences were apparent at 3 years, but no significant differences were found in analyses of 3-year heights and 3- to 6-year height increments.

Coefficients of within-plot variation in 6-year height were uniformly low in the Vicksburg planting (0.17), but averaged 0.23 on the Sewanee cove site, 0.27 on the Sewanee plateau, and 0.28 at Birmingham. The lower coefficients of variation in the Vicksburg plots are probably related to plots being in a cleared, disced field. All coefficients of variation in the test are lower than those reported by Sluder (1960) for a planting in western North Carolina.

Table 2. Juvenile height (feet) of yellow-poplar from four provenances growing at four locations

Provenance	Vicksburg		Sewanee cove		Sewanee plateau		Birmingham		Test mean	
	3 yr.	6 yr.	3 yr.	6 yr.	3 yr.	6 yr.	3 yr.	6 yr.	3 yr.	6 yr.
Sewanee, Tenn.	9	21	6	19	4	10	4	9	6	15
Oxford, Miss.	10	21	8	23	4	9	4	9	6	16
Birmingham, Ala.	8	18	7	22	6	13	5	12	6	16
Gloster, Miss.	10	22	7	21	5	12	4	10	7	16
Mean	9	21	7	21	5	11	4	10		

Foliation

The sequence of foliation was the same in all observed plantings (Table 3): trees from Gloster broke dormancy first, followed by those from Birmingham, Oxford, and Sewanee. In 1966 the Sewanee cove planting foliated a few days before the more elevated Sewanee plateau planting, and both Sewanee installations flushed earlier than the Mississippi one. This unexpected difference between the Mississippi and Tennessee foliation time is probably due to an unusually cold late March in central Mississippi. In 1967 the Vicksburg planting foliated about 4 days earlier than the one on the Sewanee plateau.

DISCUSSION

The juvenile performance of trees from all provenances has been good at all four locations. It is especially notable that the Gloster material has survived on the Cumberland Plateau, and that Sewanee trees have grown well in central Mississippi. Apparently, yellow-poplar's adaptive response to climatic variation over the test region is not great enough to penalize movement either north or south within the region.

Most of the observed variation in growth is related to site and follows a pattern which can be easily predicted, given a rudimentary knowledge of yellow-poplar site relations. All sources performed best on deep, moist, well-drained cove or creek-bottom soils. Growth has been remarkably similar on sites of generally equal quality (i.e., Sewanee plateau and Birmingham) despite major differences in their geographical location. In short, variation in growth to date seems to be related mostly to edaphic factors.

Variation in foliation dates, on the other hand, followed a pattern which has been previously observed in yellow-poplar (Sluder 1960) and other species (Kriebel and Wang 1962; Perry and Wang 1960): trees from southern sources foliate earlier, given the same environment, than those from more northern areas. This reaction is probably related to genetic differences in dormancy among populations sampled in this study.

Table 3. Mean number of days from February 28 to foliation date of yellow-poplar from four provenances growing at three locations. Means not connected by the same line are significantly different (.05 percent level).

Provenance	Vicksburg		Sewanee plateau		Sewanee cove
	1966	1967	1966	1967	1966
Sewanee, Tenn.	43	35	35	38	35
Oxford, Miss.	43	32	35	36	32
Birmingham, Ala.	41	32	33	34	25
Gloster, Miss.	33	27	26	34	21

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Epicormic Branching: A Real Problem in Plus Tree Selection

PAUL P. KORMANIK and CLAUD L. BROWN[1]

It is easier to describe those characteristics a tree must possess for incorporation in a tree improvement program if the final product is known. Selection criteria for trees destined for pulp differ in some ways from those for trees destined to become veneer. Epicormic branches would be of no consequence in selecting for rapid juvenile growth when trees will be coppiced at very short rotations, as suggested by McAlpine and Brown (1967). Unless otherwise stated, the remarks here will be confined to tree selection where the final product is assumed to be quality lumber for use in furniture or other products where a premium is placed on freedom from defect.

Epicormic branches have been a problem as long as foresters have been managing hardwoods. Many generalities have been made concerning why they arise and what can be done to minimize their occurrence. The fact remains, however, that we still do not understand the basic causes of their eruption. Many silvicultural manipulations intended to control epicormic branches at an acceptable level in natural stands are of limited value. These methods will become less valuable in the future. Why is this so? Simply because if we plan to raise genetically improved trees in the time permissible under prevailing economic conditions, we will have to utilize plantations where intensive practices are applied. Conditions in these plantings seem to be ideal for the eruption of epicormic branches.

Currently, one of the many criteria for selecting hardwood plus trees is that they have no epicormic branches. Even if the only criterion for plus tree selection was resistance to epicormic branching, we would still have difficulty selecting for this trait. This is true for three rather diverse reasons. First, we do not understand the mode of inheritance of epicormic branches. Second, we do not understand the mode of development of epicormics. Third, we are sampling at a given period in time when the selection is made, and this presupposes a status quo pattern for epicormic branch development. Evidence, however, points instead to a dynamic or constantly changing pattern which seems to be strongly influenced by tree age and size and by the effect of environmental factors that may partially or completely mask the individual tree's genetic constitution.

Epicormic branches come in two distinct sizes--long shoots and short shoots. All foresters know that the typical epicormic branches we learned about in hardwood silviculture occur as long shoots. These may occur on the boles after tree damage or stand disturbance. However, in many species the more typical expression of epicormic branching in closed stands is the occurrence of short shoots (fig. 1). Size alone is not the important

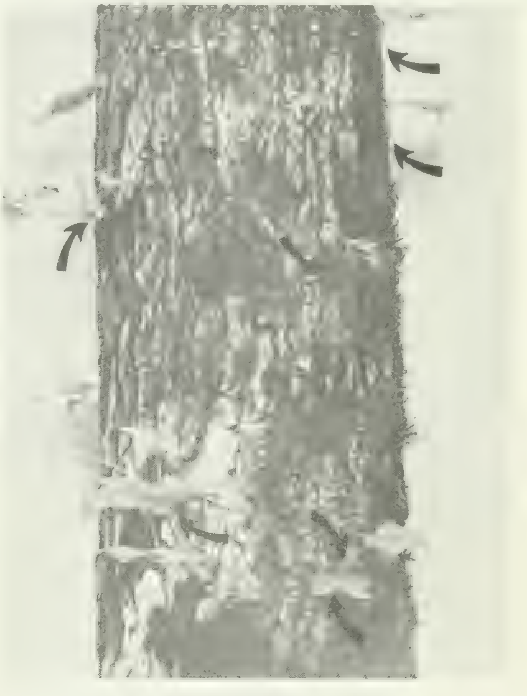

Figure 1. --Short shoots are the typical morphological expression of epicormic branches in undisturbed sweetgum stands. Longer short shoots on left side of bole illustrate environmental effect on short shoot growth habit.

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criterion for classification. The primary consideration is the amount of internodal elongation and short shoots may exist for a number of years as a stalk several inches long or be almost stalkless. In either case, they are transient in nature.

On sweetgum trees, it is not at all uncommon to find a single leaf protruding from the bark with the stalk and bud of the short shoot completely covered. In this species, it is frequently difficult to detect the presence of short shoots during the dormant season because the shoot may not be long enough at this time to extend beyond the bark crevices.

In sweetgum, it is tempting to select a "short-shootless" tree as a desirable plus tree candidate. This is especially true with the emphasis placed on a clear butt log; yet, it is this species that best exemplifies the error that can be made when we attempt to make selections at such a point in time. Sweetgum is therefore a good choice of species to discuss when presenting the problem of epicormic branching in plus tree selection.

A close look at the terminal leader of any sweetgum will reveal the ultimate source of epicormic branches in this species. At each node there is one axillary bud accompanied by two collateral accessory buds (fig. 2). These collateral accessory buds are potential producers of epicormic branches. At some nodes, buds of this type are not readily visible. However, histological examination of these nodes always reveals the presence of the axillary bud and the two bud primordia (fig. 3). The axillary buds at one time or another give rise to branches whose longevity may vary considerably. While these axillary branches function, they inhibit the two associated accessory buds. Removal of these branches results in release and growth of the accessory buds. However, natural senescence and death of the branch does not cause a similar release of bud inhibition.

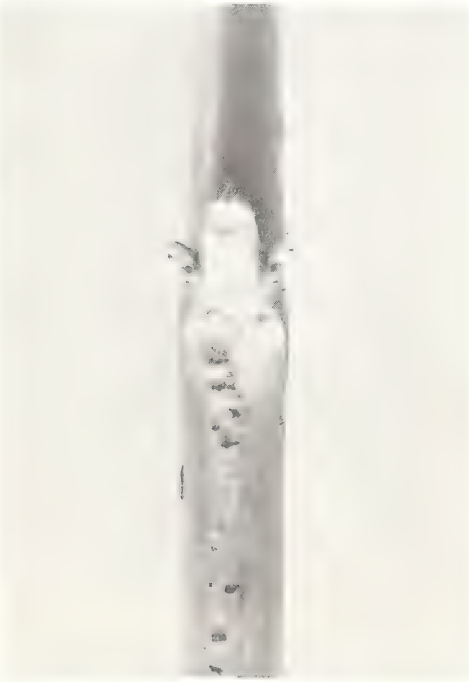

Figure 2.--Each node on the current year's leader of sweetgum characteristically develops two collateral buds which eventually become suppressed trace buds.

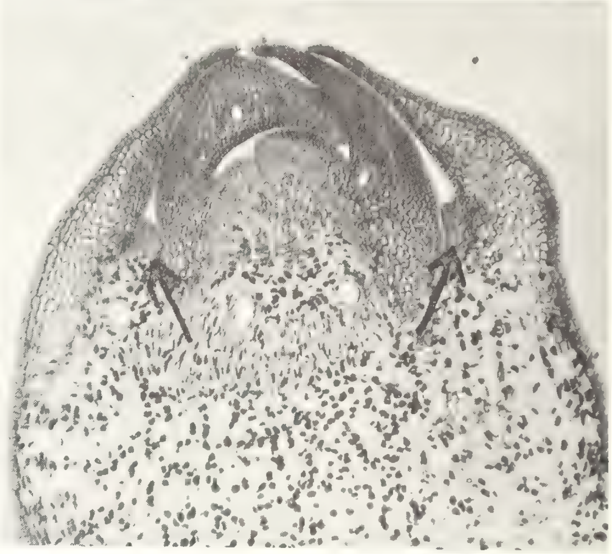

Figure 3.--Even though axillary buds are barely visible at the base of the current year's growth, accessory bud primordia (arrows) are characteristically present. X 100

As the stem increases in diameter during the early life of the tree or shoot, the two accessory buds gradually become embedded in the bark. This usually occurs from three to five years after the buds are initiated. Externally, the accessory buds seem to have aborted, but histological examination reveals that the two well-developed buds are in a transitional stage and only the external scales are being sloughed off (fig. 4). With subsequent radial growth, these buds become completely embedded in the bark. They are now referred to as dormant or suppressed trace buds (fig. 5). The number of potential suppressed buds initiated on the new terminal shoot varies. It is evident, however, that the number is related directly to the number of nodes.

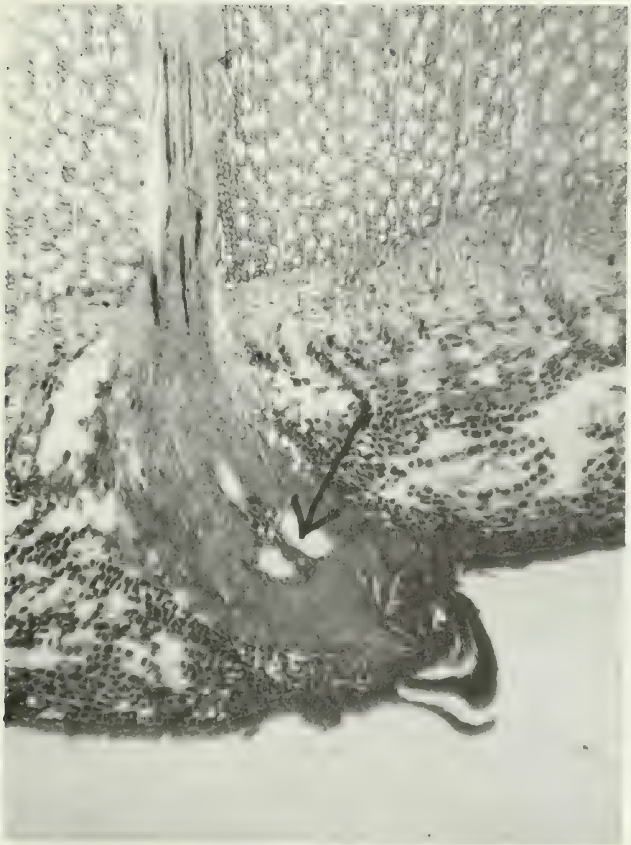

Figure 4.--Accessory buds seem to abort a few years following initiation; however, only the outer bud scales are lost and the bud itself appears to be morphologically unaffected. X 125

The final envelopment of the bud by the bark does not cause complete cessation of growth, as the name suppressed trace bud might imply. On the contrary, these suppressed buds remain physiologically active. It is well known that suppressed buds grow enough to remain outside the expanding ring of wood. But of greater importance to us is that a single suppressed bud can be the progenitor of numerous others (Kormanik and Brown, 1964). This latter phenomenon results in suppressed buds being present in increasingly large numbers as the tree matures. At various times during the life of the tree, suppressed buds are partially released from inhibition and appear as short shoots. This occurs in seemingly random fashion on the bole of the tree, even though the tree has not been damaged or otherwise disturbed. Fortunately, under these conditions the short shoots are short lived, and once established, do not usually develop into long epicormic branches. The point here is that under natural, undisturbed conditions, short shoots rather than long shoots develop. What, then, would happen if the same tree were grown in a plantation at a wider spacing so that short shoots received more sunlight? If all such short shoots elongated as much as four inches and lived for five years, the search for clear lumber would be an extremely difficult undertaking. Depending perhaps on both internal as well as external factors, a poor tree in 1960 may be classified as an excellent tree at present.

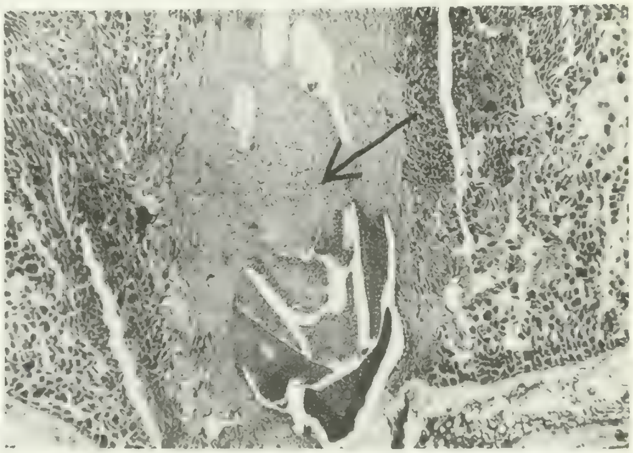

Figure 5.--Suppressed buds such as this one (arrow) are found embedded in the bark of sweetgum of all ages. X 90

Although we have not made long-term observations of short shoot development on individual trees, we have made close examinations of many individual trees over a shorter period of time. A considerable number of mature trees have been cut and the entire boles, from stump to crown, have been sectioned into ½-inch discs to ascertain the presence of suppressed buds. These observations show, first of all, that there may be a period in the tree's development when suppressed buds are prone to multiply. This seems to occur most frequently in the center 8- to 10-inch core. When a stem is within this diameter range, the eruption of a short shoot may be associated with the appearance of additional suppressed buds at the base of each short shoot (fig. 6). We are slowly gathering evidence that this bole area of maximum suppressed bud activity gradually shifts upward as the tree grows, and in time, a clear butt log is evident. Although suppressed buds are present in the butt log, the number of short shoots is greatly reduced. The physiological processes that regulate this apparent change in suppressed bud activity, or degree of inhibition, are

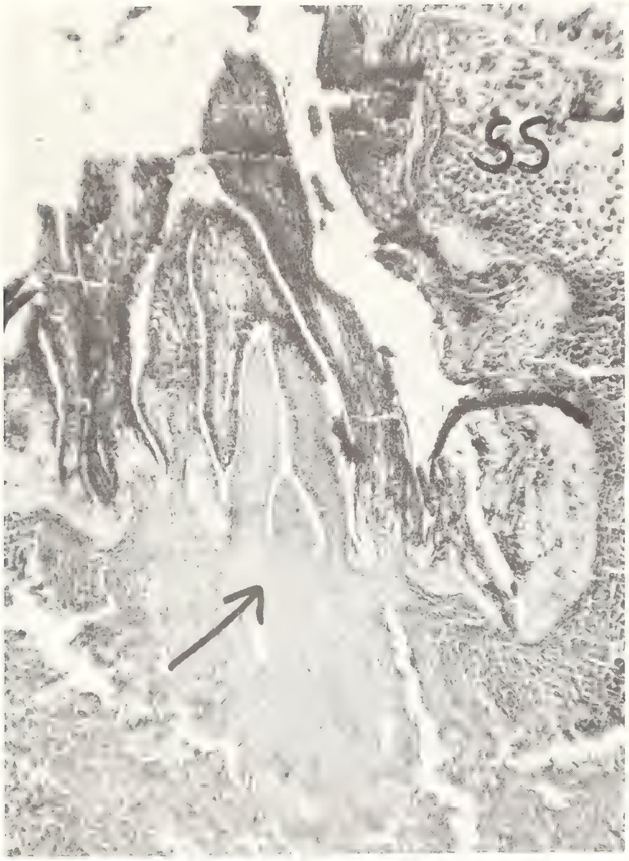

Figure 6.--The development of short shoots (SS) from suppressed buds may result in the proliferation of additional suppressed buds (arrow) that might produce additional short shoots or epicormic branches later in the life of the tree. X 120

poorly understood, as is the role that environment plays in these internal biological processes.

On the terminal leader and for some distance below it as mentioned earlier, the accessory buds, which can become suppressed buds, are inhibited by the action of the associated axillary buds, or, more correctly, by the branches that develop from the axillary. But what factors are involved in inhibition of suppressed buds on older trees after natural pruning has removed the branches low on the bole? Here, apparently, one or more inhibitory processes may be involved. The inhibition can be removed by different stimuli. The mechanisms of inhibition are not known, and in fact may vary among species. Even though our efforts have been concentrated on sweetgum, we feel that we still do not have sufficient developmental information on suppressed buds to search for differences among selected individuals. Furthermore, when one considers the magnitude of the progeny testing job and time involved to do the work, one can reasonably question the value of such an undertaking if it were based on our present knowledge.

During the past several years, we have been placing partial or complete girdles on the boles of trees of several species to determine gross patterns of suppressed bud inhibition. Results have convinced us that suppressed buds are more numerous on most trees than we originally thought. It is not unusual to count 250 epicormic branches and suppressed buds on the first 16-foot log after girdles are placed two or three feet apart along the bole of the tree. Usually, only long shoots are formed as a result of these girdles. Apparently, the girdle completely disrupts the inhibitory process.

Although these studies have shown that suppressed buds are numerous, they have also reinforced our conviction that tree improvement by judicious selection may be possible and indeed practical, for not all individuals of a species produce epicormic branches to the same degree as a result of the girdles. In fact, tree improvement of yellow-poplar may be a relatively simple task. Within this species, about 20 percent of the treated trees fail to produce epicormic branches of any consequence. If after a tree is girdled and released it still produces no epicormic branches, it is unlikely that they will develop at a later time. In fact, when we cut the first log of several such trees into thin discs, we found as few as 5 or 10 suppressed buds, and these had not been stimulated by girdling. However, when we cut several other trees which had sprouted profusely following treatment, we found up to 200 suppressed buds and epicormic branches on the first log.

An extremely interesting pattern of suppressed bud stimulation is becoming apparent through these girdling studies. That is, diffuse-porous species seem to have a different expression in the mechanism of suppressed bud inhibition than do some ring-porous species. However, we will have to treat more ring-porous species before we are certain of this. With diffuse-porous species, a single complete or partial girdle tends to stimulate epicormic branch eruption in a spirally oriented pattern that is quite similar to the tree's natural phyllotaxy. The pattern is, of course, not precise because of the phenomenon of suppressed bud multiplication. The affected area of the bole extends about two feet below the girdle (fig. 7). Usually, below this spiral no additional

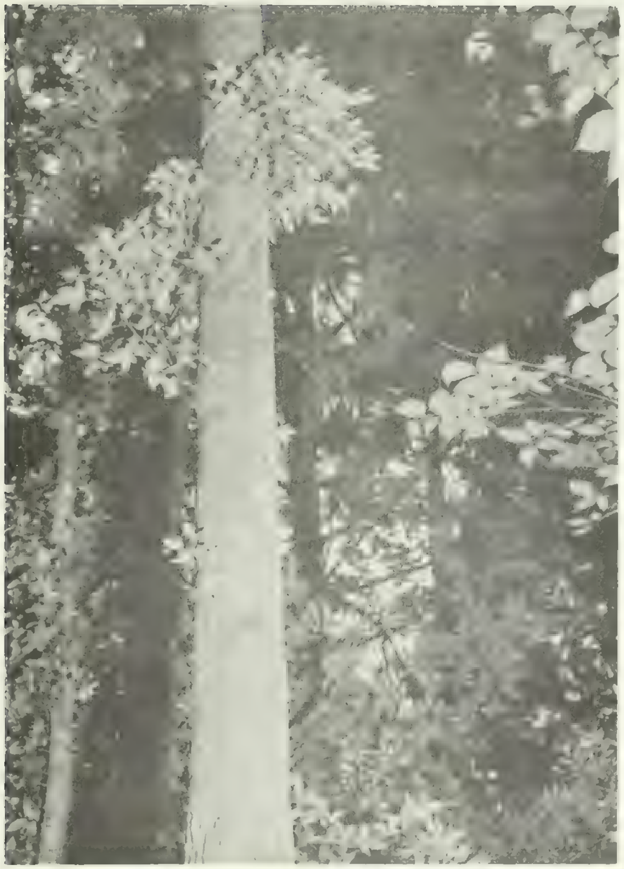

Figure 7.--Eruption of numerous suppressed buds into long epicormic branches following girdling of sweetgum. The epicormic branches show a fairly definite phyllotaxic arrangement, even on old stems.

epicormic branches develop nor are short shoots on the bole visibly stimulated.

With ring-porous oaks, more special problems concerning response to girdling have become glaring. With water oak, on which epicormic branches are frequently found, regardless of stand density, a single girdle results in suppressed bud stimulation from the girdle to the ground. All water oaks girdled exhibited this response, regardless of age or size. White oak sometimes showed the same response as water oak, but frequently failed to respond at all. When we determined the origin of epicormic branches on responsive oaks, we found that at least 30 percent of the epicormics did not have a vascular connection with the pith (Kormanik and Brown, in press 1967). When suppressed white oaks were sectioned, this percentage was much higher. Very few large dominant white oaks produced more than two or three epicormic branches, whereas the suppressed and intermediates produced 30 or more.

In sectioning several large treated white oaks, we found surprisingly few suppressed buds. We have not studied the development of suppressed buds in the oaks and know nothing about any possible developmental patterns. White oak has a reputation for developing epicormic branches; therefore, several things may be happening. Either our three stands of white oaks are completely atypical, or white oak must have a tremendous potential for developing adventitious buds when growing under adverse conditions. Also, suppressed trace buds under these adverse conditions may become quite prolific.

If we cannot look at a tree and determine its tendency towards suppressed bud inhibition, and if we do not as yet have biological procedures for determining physiological differences, what can we do? With our limited knowledge we can only suggest selection criteria for those species which we have studied. For instance, at this stage of the game, the best we can recommend for white oak is to pick strong dominants and give the progeny adequate growing space. For yellow-poplar, response to partial girdling may be an adequate test for resistance to epicormics. Although we are not prepared to set epicormic branch selection guides even for sweetgum, we are convinced that for a rotation of 45 to 50 years, trees between 20 and 30 years of age should be selected, and these should be given complete release before the final determination is made. If selection of trees, based on our present knowledge, is made for sweetgum over age 60, one might be better off to ignore epicormic branching entirely. With this species, it can be emphasized that the lack of short shoots on older trees, even two logs up, should not be construed to mean lack of suppressed buds or superiority in maintaining them in a suppressed condition.

When one considers the fundamental development of epicormic branches, without considering the possibility of inherent differences of suppressed bud inhibition, the possibilities for selective improvement seem bleak. But in reality, inherent differences do exist. It is left to us only to determine methods of ascertaining these differences. Of the species we have examined, green ash perhaps offers us the greatest reason for hope. It is only under most adverse conditions that any but the suppressed and a few intermediate trees develop epicormic branches. The dominants and codominants remain clear. Yet, partial girdles put on dominant and codominant trees produce the most vigorous epicormic branches we have ever stimulated. It is difficult to believe the ability to keep suppressed buds inhibited evolved only in green ash.

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Tubed Seedlings: A Technique for Planting Improved Stock

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Poor survival and initial height growth of certain seedling species like longleaf pine, black walnut, oak, and some others, are major problems. The ability of longleaf pine to become established on dry sand ridges, where few other species are able to survive, suggests that initial root habit of the species is important to survival. Root development and extension are rapid after the seed germinate and seedling roots may penetrate eight feet or more in 10 or 11 months (Wahlenberg, 1946). Derr (1948) found that the survival of 200 longleaf pine seedlings was closely related to the amount of lateral roots broken off in lifting from nursery beds. Height growth after six years for trees with laterals was 4.5 feet and without laterals it was 1.7 feet.

Handling of black walnut seedlings poses a problem. If the taproot is severed during lifting, rot causing fungi may enter the wound causing seedling stunting and mortality. Seedlings are generally large and difficult to handle. Height growth the first year after planting is negligible and seedlings often suffer dieback.

Studies have shown that survival and height growth of red oak and white oak seedlings are often unsuccessful (Williams, 1963). Second-year height growth of red oak ranged from 0.0 to 0.26-foot, and survival ranged from 74 to 86 percent. Seed were planted as part of the study and they grew almost twice as much in height as the transplanted seedlings.

Many nursery grown seedlings with a large root system die as a result of heavy root pruning during lifting because the root systems are not able to meet the water demand of the seedling after transplanting; consequently, the seedling suffers dieback or succumbs. Efforts to lessen the problem by direct-seeding some of the large-seeded and deep-rooted species have not been satisfactory because no repellents are yet available to keep rodents from eating seed such as acorns and walnuts.

Due to the root growth habits of many species it was conceivable that a tube-type container could be developed and used to good advantage. The idea was to plant seed in tubes, let the seedling grow several weeks, and then plant the tubed seedling. We have done some work with tubed longleaf seedlings using different kinds of tubes. The best tubes we have found thus far for this purpose are those made with kraft paper and a non-toxic water resistant glue. Two companies that specialize in making tubes or cores made some special tubes for our study.[3] We also used a polyethylene tube which another company made up for this purpose.

On April 22, 1966, tubes were filled with a mixture of perlite, peat, sand, and soil and then a seed was placed in each tube. About eight weeks later we planted the tubling in a Lakeland loamy sand in south Georgia. Treatments were:

A. Kraft paper tubes, 1-inch i.d. x 10 inches long.
B. Kraft paper tubes, 1½ inches i.d. x 10 inches long.
C. Polyethylene tubes, 7/8-inch i.d. x 10 inches long, solid.
D. Polyethylene tubes, 7/8-inch i.d. x 10 inches long, with two 8-inch slits.
E. Polyethylene tubes, 7/8-inch i.d. x 10 inches long, with twelve 1/4-inch holes.

*A special planting tool was made to plant them.

The seed germinated and the roots of the resulting seedlings grew 10 inches within a 5-week period. In December 1966, six months after planting, survival ranged from 52 percent in polyethlene tubes with holes to 92 percent in 1-inch kraft tubes (table 1). Some of the tubes and seedlings were dug up with as much of the root as possible and most of the taproots were over two or three feet long.

The kraft tubes decomposed rapidly after planting. Root growth was hampered little, and some of the lateral roots went through the wall of the kraft tubes.

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[3] One-inch tubes made by Sonoco Products Co., Hartsville, S. C.; 1½-inch tubes made by Textile Paper Products Company, Cedartown, Ga.

The good survival in the kraft tubes is probably due in part to the uninterrupted root growth which permitted the taproot to continue rapid downward growth and reach moisture. If planting is delayed more than two to three months, this rapid taproot growth may be hampered.

Based on the results of these studies, it appears that a kraft paper tube made with a water resistant, non-toxic adhesive is an excellent carrier for longleaf pine, oak, walnut, and other deep-rooted seedlings.

Table 1.--Average survival of two-month-old tubed longleaf seedlings planted June 15.

Tube Description	Survival percentage	
	August	December
Kraft, 1-inch i.d.	92	92
Kraft, 1-½-inch i.d.	95	88
Polyethylene, solid	84	84
Polyethylene, slit	79	67
Polyethylene, holes	61	52

Due to the persistency of the polyethylene and possible hindrance to root growth, the polyethylene tube cannot be recommended until further results are obtained.

The growing of seedlings in tubes and planting soon after root growth begins offer many advantages, especially in tree improvement work where you want as much uniformity as possible in growing and transplanting seedlings.

ADVANTAGES ASSOCIATED WITH PLANTING TUBED SEEDLINGS

1. The tube method permits the young seedling to begin and maintain rapid root growth in a near natural condition.

2. The V-shaped and L-shaped root caused by planting would not be a problem.

3. One could better schedule seeding and planting to coincide with the species ecology.

4. If demands exceed seedling supply, the tube method would offer a solution since only a few weeks are required from time seed are planted until seedlings are ready to plant.

5. Tubed seedlings offer an opportunity for planting during most of the year.

6. A nursery is not needed; therefore, seedling production could be on a local basis. Expenditures for nursery equipment and facilities are not needed.

7. The tube offers a good potential for mechanization in production of seedlings and in planting of the tublings.

8. Initial seedling development and growth may be improved by the use of special mixed media and fertilizer in the tubes. The addition of systemic pesticides is a possibility.

9. Another advantage of tublings is in studies where 100 percent survival is required. Tubed seedlings in excess of immediate study needs could be prepared and used for replants if some of the original plants died.

10. If seedlings need to be marked, a flag or a marker can be placed in the tube prior to planting.

DISADVANTAGES OF PLANTING TUBED SEEDLINGS

1. The major disadvantage to the tubes at the present time is their cost. Quotations have been $0.013 to almost $0.03 each, depending on size and amount. This cost may be offset somewhat by mechanization, increased survival and improved growth. Cost would be easily justified, however, in research studies.

2. Another disadvantage is transportation and handling of the tubes and tubed seedlings. Until a planting machine is developed and used, planting may be slower than the planting of bare-root stock.

PRECAUTIONS REQUIRED FOR SUCCESSFUL USE OF TUBED SEEDLINGS

1. When ordering tubes, one should be sure to specify that they be made with a water resistant glue and that the glue be non-toxic to plants. Also, the paper should be of a fairly good quality.

2. The tube should be almost completely filled with the medium, with the seed placed on top and lightly covered. The medium should be placed in the tubes in such a way that it will not settle to cause the seedling to be recessed in the tube more than ½-inch.

3. During and immediately after germination, seedlings may need general control measures for damping-off fungi, such as **Fusarium** spp.

4. The seedlings should be outplanted as soon as, or just prior to, the taproot reaching the end of the tube; otherwise, some of the advantage of the tubed seedling may not be realized because taproot growth may be disturbed or lost at planting time.

5. When planted, the tube should be flush with the ground line. If the tube protrudes above the ground line, it may act as a wick and cause a dry condition around the newly planted seedling roots.

6. Avoid planting on sites after extensive site preparation until the soil has settled.

The use of tubes can be a valuable aid in artificial regeneration, especially in the regeneration of our more important and improved hardwoods.

Tubes could also be used in rooting of cuttings. After root initiation, the cutting and tube could be planted without disturbance to the root as is the case when lifted from a rooting bed.

A Study of Racial Variation in Loblolly Pine in Georgia--Tenth-Year Results

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The Georgia Loblolly Pine Racial Variation Study was designed to complement the Southwide Pine Seed Source study[2] by testing samples of loblolly pine seed, from collections made in all provinces of Georgia, in plantations established throughout the state.[3] It has performed this function in a most admirable fashion. In general, the results do not conflict in any way with those recently reported on the tenth-year results of the loblolly phase of the Southwide Pine Seed Source Study (Wells and Wakeley, 1966). Basically, the data obtained in the Georgia study indicate that the variation in the growth of loblolly pine from different parts of the state is of sufficient magnitude that it will require consideration in seed procurement and planting plans. It is an important factor in the seed orchard program of the Georgia Forestry Commission.

STUDY DESCRIPTION AND HISTORY

In the fall of 1954, cones were collected from between 20 and 26 trees in each of 14 collection areas in Georgia (figure 1). One collection was made from each of six Georgia Forestry Commission forestry districts, and two collections were made from the remaining four forestry districts. In addition to the 14 collections from Georgia, three lots were obtained from north Florida and one from Arkansas table 1).

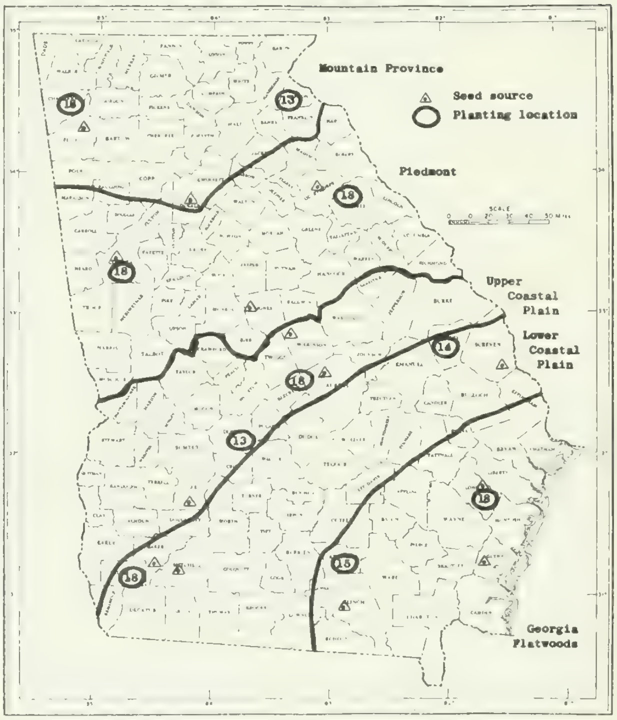

Figure 1. Location of 14 loblolly pine seed sources and 10 planting locations in Georgia. (ⓝ= number of seed sources in plantation)

In the spring of 1955, the seed were sown in the Georgia Forestry Commission's Davisboro Nursery in a randomized block design with two replications. The seedlings were machine lifted in December 1955; bundles made up by plot, block, and plantation; and all necessary stock, including border-row seedlings, were shipped to the cooperators.

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[2] The Southwide Pine Seed Source Study is a cooperative study of the geographic variation of the four major southern pines sponsored by the Committee on Southern Forest Tree Improvement.

[3] Cooperators in this study are: the Georgia Forestry Commission, Union Camp Corporation, Georgia Kraft Company, International Paper Company, Georgia National Forests, Champion Papers Incorporated, and the Georgia Forest Research Council.

Table 1.--Sources of 18 loblolly pine seed lots used in the Georgia Study

PROVINCE	COUNTY	NEAREST TOWN
Mountain	Floyd	Shannon
"	DeKalb	Stone Mountain
Piedmont	Oglethorpe	Lexington
"	Coweta	Newnan
"	Jones	Wayside
Upper Coastal Plain	Wilkinson	Gordon
"	Laurens	Dublin
"	Lee	Leesburg
Lower Coastal Plain	Screven	Halcyondale
"	Baker	Newton
"	Mitchell	Cotton
Flatwoods	Clinch	Homerville
"	Long	Walthourville
"	Glynn	Waynesville
Florida	Baker	Taylor
"	St. Johns	Palm Valley
"	Walton	DeFuniak Springs
Arkansas	Ashley	Crossett

Plantations were established at 10 locations. They were as uniformly distributed throughout the state as the availability of cooperators made possible (figure 1). All 18 seed sources were used at six of the plantations. Due to shortages in planting stock, two plantations contained only 13 sources while the other two each contained 14 and 15 sources. The three north Florida seed sources were planted in both of the Piedmont plantations but only at one location in each of the other four physiographic provinces.

A randomized complete block design was used with four replications of 36-tree-square plots planted at a spacing of 10 x 10 feet. A two-row border strip of commercial stock was planted around all outside boundaries.

With one exception, all the plantations have been remarkably free of damage by fire or man. The plantation in Long County sustained some cattle damage during the first few years, and two corner plots were damaged by site-preparation equipment. Even in these plots, however, sufficient trees remained to permit measurement of heights and fusiform rust (**Cronartium fusiforme** Hedgc. & Hunt ex Cumm.) infection.

During the winter of 1965-66, when the trees were 11 years old from seed, measurements were taken at all plantations of the 16 trees in the center of each plot. Survival, total height, d.b.h., and the incidence of fusiform rust stem cankers and branch galls were recorded on IBM Mark Sense Cards. These cards were processed in the facilities of the Georgia Forestry Commission, and all analyses have been made on plantation-seed source means.

Cubic-foot volume growth was calculated on an individual tree basis using the formula for a cone having a height equal to the plot mean total height and a basal area equal to that at breast height. This value was also used to estimate volume production on a per acre basis in which survival was also a variable.

ANALYSIS AND RESULTS

The principle analysis used combined the data from all plantations for the 14 Georgia seed sources (table 2). In this analysis the state was divided into five physiographic provinces, each containing two plantations (figure 1). The four southern provinces were sampled by three seed sources, while the mountain province was sampled by two.

For each trait, the average values by seed source province and planting province are summarized in table 3. For example, the entry under the piedmont seed source province for the Georgia flatwoods planting province is the mean of six values (three piedmont seed sources planted in two Georgia flatwoods locations). All tests of statistical significance were at the .01 level because there were no comparisons that differed only at the .05 level.

DIFFERENCES AMONG PLANTING PROVINCES

There were no statistically significant differences among the five provinces for any of the traits examined with respect to the overall performance of the Georgia seed sources. Despite the lack of statistical significance, there were two noticeable tendencies. Rust infection and mortality were lowest in the mountain province, and as a consequence, volume production was highest in that area (table 4). In the piedmont, volume growth excelled that of the other provinces as a result of that province producing trees with the best average heights and diameters (table 4). Whether these tendencies are meaningful can best be judged on the basis of the results which follow.

Table 2.--Analysis of variance and mean squares for tenth-year survival, fusiform rust infection height, d.b.h., volume growth and volume production

Source of variation		Degrees of freedom	Mean squares						E(MS)
			Survival	Rust infection	Height	D.b.h.	Volume growth	Volume production	
Planting province	A	4	1,342.64	7,257.31	164.20	6.66	6.21	541,980	$\sigma_e^2 + 2\sigma_{as(b)}^2 + 14\sigma_{l(a)}^2 + 28\theta_a^2$
Locations in province	L(A)	5	1,092.22**	1,908.22**	51.48	3.08**	2.38**	150,842**	$\sigma_e^2 + 14\sigma_{l(a)}^2$
Seed source province	B	4	613.25**	143.31	48.93	1.67**	1.73**	9,911	$\sigma_e^2 + 2.8\sigma_{bl(a)}^2 + 10\sigma_{s(b)}^2 + 30\theta_b^2$
Seed sources in province	S(B)	9	107.77**	263.45**	1.94	0.21	0.11	11,706	$\sigma_e^2 + 10\sigma_{s(b)}^2$
A x B		16	55.80	25.14	16.00	0.41	0.46	57,266	$\sigma_e^2 + 2\sigma_{as(b)}^2 + 2.8\sigma_{bl(a)}^2 + 5.6\sigma_{ab}^2$
A x S(B)		36	28.33	30.93	1.90	0.12	0.08	7,029	$\sigma_e^2 + 2\sigma_{as(b)}^2$
B x L(A)		20	26.91	53.99	1.71	0.08	0.08	7,849	$\sigma_e^2 + 2.8\sigma_{bl(a)}^2$
S(B) x L(A)		45	25.24	40.74	2.29	0.11	0.07	9,434	σ_e^2

**Significant at the 0.01 level.

DIFFERENCES BETWEEN PLANTING LOCATIONS WITHIN PROVINCES

Within each of the major physiographic provinces, there were plantations at two locations (figure 1). There were highly significant differences between these plantations for all traits, indicating that site, planting procedure, and other local factors were more important than the location of the plantation. Only in the case of rust infection do the data seem to warrant qualification since, despite the lack of statistically significant differences between provinces, rust infection was much lower in both plantations in the mountains. It appears that only the large variation between plantations in the other provinces prevented this difference being significant. The incidence of rust in the most heavily infected of the two mountain locations (Stephens County) was only 12 percent, compared to 42 percent in the next least infected plantation (Dooly County), located in the upper coastal plain.

DIFFERENCES AMONG SEED SOURCE PROVINCES

There were highly significant differences among the five provinces as seed source in survival, height, diameter, and volume growth (table 2). Although the magnitude of these differences was not large for all traits, their trends were rather consistent.

Survival averaged over all plantations was highest for the mountain seed sources (80 percent) and got progressively poorer for each of the southern provinces, averaging 62 percent for the sources from the Georgia flatwoods.

The trend was reversed for height, diameter, and volume growth. The best performance for these traits was attained by trees from the Georgia flatwoods sources and tended to decrease in each succeedingly more northerly province (table 5).

There was a slight tendency for rust infection to be lowest among trees from the mountain seed sources and highest among trees from sources in the Georgia flatwoods, but the differences were neither large enough nor the trend consistent enough to attain statistical significance.

Although it was not included in the analysis of the combined data from the Georgia sources, the performance of the single source from Arkansas was interesting. Trees from this source were unexcelled in survival and resistance to rust infection (table 5). Their exceptional rust resistance throughout the state reinforces previous reports of the low susceptibility to fusiform rust infection of the western sources of loblolly pine (Wakely, 1944, 1961; Bethune and Roth, 1960; Wells, 1966; Wells and Wakeley, 1966). In height, diameter, and volume growth they were intermediate of trees from the piedmont and mountain sources. Due to its high survival and rust resistance, this source produced the highest volumes per acre in all but the mountain and flatwoods provinces (table 3).

The performance of the three north Florida sources is difficult to evaluate since in three of the four provinces in which they were only planted at one location, that location had the poorer average growth for all seed sources. Several correction fac-

Table 3.--Average performance of loblolly pine seed lots grouped by seed source provinces and planting provinces

Planting Province	Seed Source Province 1/ Florida	Georgia Flatwoods	Lower Coastal Plain	Upper Coastal Plain	Piedmont	Mountain	Arkansas
				Survival-percent			
Georgia Flatwoods	38.8	59.4	67.3	74.6	72.6	71.5	84.7
Lower Coastal Plain	59.8	60.7	65.3	69.7	66.9	78.1	85.7
Upper Coastal Plain	53.2	66.5	68.0	67.2	75.4	82.5	95.1
Piedmont	46.5	48.1	48.6	59.2	72.5	74.1	77.9
Mountain	79.7	76.5	82.1	87.9	96.2	91.8	98.8
				Fusiform rust infection-percent			
Georgia Flatwoods	90.2	67.6	61.3	63.3	63.6	51.0	14.2
Lower Coastal Plain	92.0	76.5	72.4	73.1	72.5	68.6	21.1
Upper Coastal Plain	89.0	68.0	64.6	62.1	68.2	59.3	9.4
Piedmont	83.1	76.5	59.1	59.6	61.3	62.6	7.8
Mountain	23.3	12.6	9.2	12.6	8.6	8.8	0.1
				Height-feet			
Georgia Flatwoods	26.9	33.3	30.2	29.9	26.8	24.4	28.0
Lower Coastal Plain	31.8	33.3	32.0	31.2	28.2	28.2	29.7
Upper Coastal Plain	26.4	26.0	26.1	26.3	24.9	23.9	25.2
Piedmont	32.8	33.2	32.0	32.9	30.5	30.4	31.2
Mountain	28.4	28.6	29.6	30.7	32.1	30.3	28.6
				D.B.H.-inches			
Georgia Flatwoods	5.6	6.4	5.7	5.7	5.3	4.7	5.4
Lower Coastal Plain	6.4	6.6	6.5	6.2	5.9	5.8	6.1
Upper Coastal Plain	6.1	5.6	5.7	5.7	5.4	5.2	5.2
Piedmont	6.8	7.0	7.0	6.8	6.4	6.4	6.3
Mountain	5.9	6.1	6.2	6.2	6.4	6.3	6.0
				Volume growth-cubic feet			
Georgia Flatwoods	1.74	2.60	1.92	1.82	1.46	1.10	1.52
Lower Coastal Plain	2.42	2.68	2.47	2.22	1.83	1.75	1.99
Upper Coastal Plain	1.78	1.50	1.55	1.61	1.35	1.19	1.26
Piedmont	2.78	2.96	2.96	2.97	2.30	2.26	2.30
Mountain	1.80	1.96	2.10	2.20	2.43	2.17	1.87
				Volume production-cubic feet/acre			
Georgia Flatwoods	307	676	574	584	473	331	532
Lower Coastal Plain	608	678	681	655	515	582	730
Upper Coastal Plain	400	420	420	444	374	395	508
Piedmont	531	566	600	630	690	712	744
Mountain	626	627	739	798	986	817	791

1/ The three Florida sources are represented in both Piedmont plantings but in only one plantation in each of the other provinces.

tors were tried on these data to see if they might better fit the growth trends established by the Georgia sources. Since the corrected values did not change the relative values appreciably, they have been left uncorrected in tables 3 and 5, and in figure 2. In general, trees from the Florida sources grew slightly slower than trees from sources in the Georgia flatwoods and coastal plain, and sustained slightly higher mortality and rust infection.

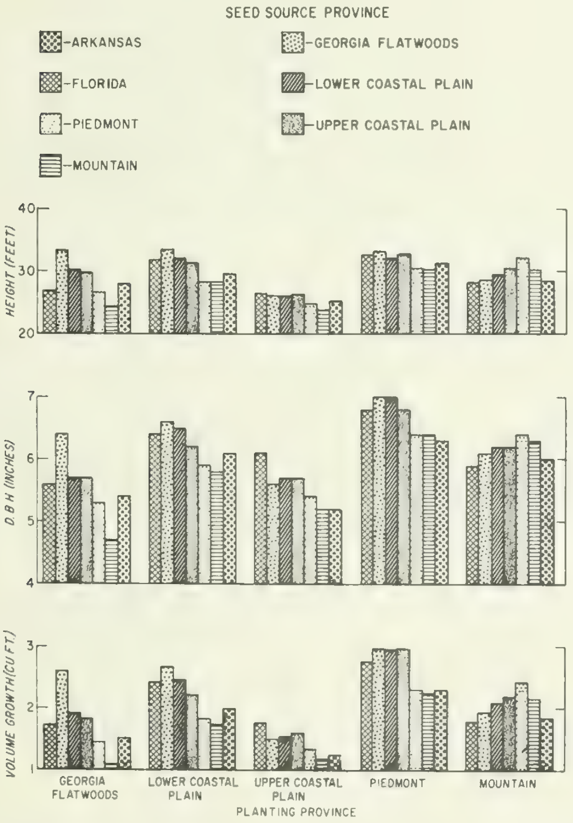

Figure 2 - Average height, d.b.h., and volume growth of loblolly pine from seven source provinces planted in five Georgia provinces.

SEED SOURCE DIFFERENCES WITHIN PROVINCES

There were highly significant differences between seed sources within the five major seed collecting provinces in only two traits, survival and rust infection. In the case of survival it is probably best not to place too much weight on these results. Two factors suggesting this interpretation are: (1) the fact that in the Georgia study the seed source with the poorest average survival was not poorest at all locations nor was the best source best at all locations, and (2) too large a portion of the variation in survival may be associated with nursery environment and outplanting procedures.

Differences in rust infection among seed sources were probably less influenced by external factors in this study. The results show that detectable genetic differences exist between specific seed sources in Georgia. These differences are randomly distributed rather than being strongly associated with the major seed source provinces. On the basis of other studies it is entirely possible that a portion of the variation among seed sources is due to the variation between families sampled at each seed source (Barber, 1966).

The least infected seed source in this study consistently had the lowest infection at all planting locations. However, the converse was not true with respect to the most heavily infected source.

THE INTERACTION BETWEEN PLANTING PROVINCE AND SEED SOURCE PROVINCE

The interaction between planting province and seed source province was highly significant for height, diameter, volume growth, and volume production. This interaction is most noticeable in the poor performance of trees from the piedmont and mountain sources when planted in the flatwoods and coastal plain provinces, and the relatively good performance of trees from the flatwoods and coastal plain sources everywhere except in the mountains (table 3, figure 2).

In the Georgia flatwoods the average growth of the local seed sources was noticeably superior to all the non-local sources. When only the Georgia seed sources are considered, trees from the local sources produced the highest volumes per acre in all but the piedmont and mountain provinces (table 3).

GENERAL PERFORMANCE OF THE SEED SOURCES

If the average performance over all locations of the trees from the various sources is plotted on a map at their point of origin, a general trend develops. This trend is shown for height, d. b. h., and volume growth in figure 3, where the average values for the 14 Georgia seed sources are plotted along a transect running from the northwestern corner of Georgia southeast to the Atlantic coast at the southern corner of Camden County. This transect was chosen in preference to a straight north-south line because it comes closer to being at a right angle to a number of biologically important variables, such as physiographic province, altitude, average January temperature, the average number of days without a killing frost, and the average warm season precipitation. The general trend along this transect is definitely clinal, with the values for all growth components increasing from northwest to southeast across the state. There is a slight tendency for this cline to be "stepped" as it crosses the fall line, with generally higher values below the fall line than above it.

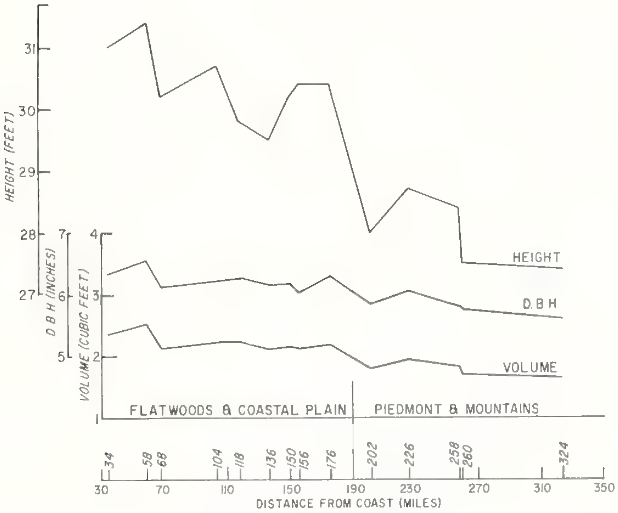

Figure 3 - Trend along a SE-NW transect of growth of 14 Georgia seed sources averaged over 10 plantations.

DISCUSSION

To the forest manager, these results may at first present a dilemma; that is, the fast growing trees from the southern sources are generally less adaptable from the standpoint of initial survival and fusiform rust resistance than the slower growing northern sources. Stand density, however, is one of the more easily controlled factors in plantation management, and given a seed source with with good growth characteristics, it would take only a slightly closer initial spacing to assure a productive, well-stocked stand. Conversely, given a seed source with known good resistance to fusiform rust, many foresters might wish to give serious consideration to a western source, such as that from Arkansas, at the risk of some loss in individual tree performance. Information on total volume yield in relation to specific gravity of wood may be obtained later.

From the standpoint of height, diameter, and individual tree volume growth, the results of the Georgia study clearly show that as far north as the upper coastal plain either the local source or one from the south would be preferable. In the piedmont, trees from the southern sources also grew best and should out-yield the local sources if adequate initial survival is obtained.

In the mountain province, trees from the local sources were inferior in all traits to those from the piedmont, but were generally superior, or nearly equal, to any source from below the fall line.

In the Southwide Study, growth decreased with

Table 4. -- Average performance (in the five physiographic provinces) of the 14 loblolly pine seed sources from Georgia

Planting Province	Survival	Fusiform rust infection	Height	D.B.H.	Volume growth	Volume production per acre
	percent	percent	feet	inches	cu. ft.	cu. ft.
Georgia Flatwoods	69.0	62.1	29.2	5.6	1.83	542
Lower Coastal Plain	67.6	73.0	30.8	6.2	2.22	625
Upper Coastal Plain	71.3	64.8	24.6	5.6	1.46	412
Piedmont	59.7	64.1	31.9	6.7	2.72	634
Mountains	87.5	10.4	30.3	6.3	2.17	792

Sixth-Year Results from a Yellow-Poplar Provenance Test

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Yellow-poplar (**Liriodendron tulipifera** L.), one of the South's most widely planted hardwoods, is the subject of intensive research in management and genetic improvement. The association of genetic variation with geographical source is important to both breeding and cultural efforts. Some reported data on racial variation in yellow-poplar fall within a pattern now generally predictable for wide-ranging woody species: Frost damage to material planted in the Midwest is greater in stock from southern than from nothern sources (Funk 1958) and frost damage limits major northward movement of planting stock. This relationship hinges upon genetic variation in photoperiodic response (Vaartaja 1964).

In an Ohio study of racial variation in first-year growth, plants from southern sources were among the largest (Limstrom and Finn 1956). Lotti (1955) observed that 3-year-old Coastal Plain yellow-poplar was taller than yellow-poplar from western North Carolina when both were planted in a small unreplicated test near Charleston, South Carolina. On the other hand, in two replicates of 16 sources (Mississippi to Michigan) planted in western North Carolina, Sluder (1960) found no statistically significant racial differences in 5-year height. Variation in dates of bud-break and growth cessation followed expected patterns, however, with trees from northern sources beginning growth later and ending it earlier than those from southern provenances.

In our study, juvenile growth of yellow-poplar from Coastal Plain and Cumberland Plateau sources has been observed in four plantings near seed origins.

METHODS

Material

In the fall of 1959, seed was collected from four sources:

(1) 10 trees on the University of the South Forest, Sewanee, Tennessee (lat. 35°30', elevation 1,500-1,800 ft.)

(2) 9 trees on the Tallahatchie Experimental Forest, Oxford, Mississippi (lat. 34°30', elevation 200-400 ft.)

(3) 20 trees on the Flat Top Experimental Forest, Birmingham, Alabama (lat. 33°30', elevation 400-600 ft.)

(4) 20 trees on the Homochitto National Forest, Gloster, Mississippi (lat. 31°30', elevation 100-200 ft.)

Trees had average to good form and growth and represented several stands in each of the general collection areas.

Bulked seed from each source was shipped to Stoneville, Mississippi, where it was stratified from late November until late March 1960. Seed from the four provenances was then shipped to cooperators who grew seedlings for their respective plantings. Seedlings for two plantings near Sewanee, Tennessee, were grown at the TVA nursery, Clinton, Tennessee. Material for plantings near Birmingham, Alabama, and Vicksburg, Mississippi, was grown near planting sites.

Planting Sites

At Sewanee, seedlings from the four provenances were planted on a plateau and a cove site on the University of the South Forest. The plateau-top site (elevation 1,850 ft.) lies on a 4-percent east slope and is characterized by a uniform Hartsells fine sandy loam; depth to bedrock is 36 to 48 inches. The cove installation (elevation 1,540 to 1,620 ft.) is on a northwest-facing site with an overall slope of 40 percent; plots are on benches with slopes of 5 to 15 percent. The soil is a Jefferson bouldery colluvium derived primarily from sandstone. Depth to bedrock is extremely variable but averages 20 feet or more. Site preparation on both of these areas consisted of chemically killing all hardwood trees and brush.

The test is replicated near Birmingham in small upland hollows (elevation 490-560 ft.) on the Flat Top Experimental Forest. Soils on the plots are Montevallo or Muskingum silt loams ranging from 2 to 4 feet in depth; slopes are moderate. The planting areas were cleared of a mixed stand of pine and hardwoods, and hardwood stumps were treated with silvicide to prevent sprouting.

The planting at Vicksburg is in a gently sloping field (elevation 200 ft.) adjacent to a moderate-sized intermittent creek. The soil is deep Adler silt loam. The site was disced in preparation for planting.

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[1] Southern Forest Experiment Station, Forest Service, U. S. Department of Agriculture. Farmer and Krinard are stationed at the Southern Hardwoods Laboratory, maintained at Stoneville, Mississippi by the Southern Forest Experiment Station in cooperation with the Mississippi Agricultural Experiment Station and the Southern Hardwood Forest Research Group. Russell is stationed at the Sewanee Silviculture Laboratory, maintained at Sewanee, Tennessee, by the Southern Forest Experiment Station in cooperation with the University of the South.

Climatic conditions in three planting areas are tabulated below. No data are available for the Sewanee cove area.

Planting localities	Mean number frost-free days	Temperatures, °F		Annual rainfall, inches
		January average	July average	
Sewanee (Plateau)	201	39	75	56
Birmingham	241	46	80	54
Vicksburg	252	50	81	49

Design and Establishment

Seedlings (1-0) were bar-planted during the winter of 1961 in randomized block designs with four replications at all four locations. Each plot contained 121 seedlings at 5- by 5-foot spacing. Blocks were planted contiguously on the Sewanee plateau and Vicksburg sites. On the Sewanee cove and Birmingham sites, uneven topography necessitated separating blocks by distances of up to ½ mile.

Maintenance and Observations

Weeds in the Vicksburg planting were mowed four times during the first growing season and twice during the second. Competitive growth at the other three sites was not cut. Height and survival after 3 and 6 years' growth were recorded for a central square of 49 trees in each plot. In 1966, foliation dates of 5 trees per plot were observed at Vicksburg and of 2 trees per plot in both Sewanee installations. Foliation of four trees per plot was observed in 1967 at Vicksburg and in the Sewanee plateau planting. Foliation date was defined as the first date on which one or more leaves were completely out of buds, and was recorded as number of days after February 28.

Analysis of variance in all characters took the form of a split-plot design with planting locations as major plots and provenance as subplots. Plot means were the units of analysis.

RESULTS

Survival

Mean 3-year survival of seedlings from provenances represented in the four plantings varied from 75 to 97 percent (Table 1). Survival was lowest (77 percent) at Birmingham and highest (96 percent) on the Sewanee plateau site. In the Sewanee cove planting, trees from the Sewanee source survived less well than those from the Oxford source (.05 level of significance); source differences were nonsignificant at other locations. Increase in mortality between 3 and 6 years was 3.6 percent points on the Sewanee cove site and less than 1 percent in the other plantings. No evidence of cold damage to stems has been observed in any of the plantings, although apices of Gloster seedlings grown at Clinton, Tennessee, were killed by frost in the nursery. Late spring frosts have occasionally caused slight leaf damage in Sewanee plantings.

Table 1. Survival at 3 years of yellow-poplar from four provenances growing at four locations

Provenance	Vicksburg	Sewanee cove	Sewanee plateau	Birmingham
	....	Percent	....	
Sewanee, Tenn	87	83	93	82
Oxford, Miss.	93	95	97	75
Birmingham, Ala.	87	90	96	78
Gloster, Miss.	91	91	96	75
Mean	90	90	96	77

Growth

Mean 6-year heights for the Vicksburg and Sewanee cove plantings were both 21 feet, and heights at Birmingham and Sewanee plateau locations were approximately one-half that (Table 2). Three-year heights followed a similar pattern. These differences in growth on the two groups of sites (Vicksburg and Sewanee cove; Birmingham and Sewanee plateau) were statistically significant (.05 level) for 3- and 6-year heights and the 3- to 6-year height increment.

Source means based on combined data from all four plantings were practically identical. However, comparison of means within locations revealed the following significant differences (.05 level) in 6-year heights:

Gloster > Birmingham at Vicksburg

Oxford > Sewanee at Sewanee cove

Birmingham > Oxford at Sewanee plateau

Trends leading to these differences were apparent at 3 years, but no significant differences were found in analyses of 3-year heights and 3- to 6-year height increments.

Coefficients of within-plot variation in 6-year height were uniformly low in the Vicksburg planting (0.17), but averaged 0.23 on the Sewanee cove site, 0.27 on the Sewanee plateau, and 0.28 at Birmingham. The lower coefficients of variation in the Vicksburg plots are probably related to plots being in a cleared, disced field. All coefficients of variation in the test are lower than those reported by Sluder (1960) for a planting in western North Carolina.

Table 2. Juvenile height (feet) of yellow-poplar from four provenances growing at four locations

Provenance	Vicksburg		Sewanee cove		Sewanee plateau		Birmingham		Test mean	
	3 yr.	6 yr.	3 yr.	6 yr.	3 yr.	6 yr.	3 yr.	6 yr.	3 yr.	6 yr.
Sewanee, Tenn.	9	21	6	19	4	10	4	9	6	15
Oxford, Miss.	10	21	8	23	4	9	4	9	6	16
Birmingham, Ala.	8	18	7	22	6	13	5	12	6	16
Gloster, Miss.	10	22	7	21	5	12	4	10	7	16
Mean	9	21	7	21	5	11	4	10		

Foliation

The sequence of foliation was the same in all observed plantings (Table 3): trees from Gloster broke dormancy first, followed by those from Birmingham, Oxford, and Sewanee. In 1966 the Sewanee cove planting foliated a few days before the more elevated Sewanee plateau planting, and both Sewanee installations flushed earlier than the Mississippi one. This unexpected difference between the Mississippi and Tennessee foliation time is probably due to an unusually cold late March in central Mississippi. In 1967 the Vicksburg planting foliated about 4 days earlier than the one on the Sewanee plateau.

DISCUSSION

The juvenile performance of trees from all provenances has been good at all four locations. It is especially notable that the Gloster material has survived on the Cumberland Plateau, and that Sewanee trees have grown well in central Mississippi. Apparently, yellow-poplar's adaptive response to climatic variation over the test region is not great enough to penalize movement either north or south within the region.

Most of the observed variation in growth is related to site and follows a pattern which can be easily predicted, given a rudimentary knowledge of yellow-poplar site relations. All sources performed best on deep, moist, well-drained cove or creek-bottom soils. Growth has been remarkably similar on sites of generally equal quality (i.e., Sewanee plateau and Birmingham) despite major differences in their geographical location. In short, variation in growth to date seems to be related mostly to edaphic factors.

Variation in foliation dates, on the other hand, followed a pattern which has been previously observed in yellow-poplar (Sluder 1960) and other species (Kriebel and Wang 1962; Perry and Wang 1960): trees from southern sources foliate earlier, given the same environment, than those from more northern areas. This reaction is probably related to genetic differences in dormancy among populations sampled in this study.

Table 3. Mean number of days from February 28 to foliation date of yellow-poplar from four provenances growing at three locations. Means not connected by the same line are significantly different (.05 percent level).

Provenance	Vicksburg		Sewanee plateau		Sewanee cove
	1966	1967	1966	1967	1966
Sewanee, Tenn.	43	35	35	38	35
Oxford, Miss.	43	32	35	36	32
Birmingham, Ala.	41	32	33	34	25
Gloster, Miss.	33	27	26	34	21

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Epicormic Branching: A Real Problem in Plus Tree Selection

PAUL P. KORMANIK and CLAUD L. BROWN[1]

It is easier to describe those characteristics a tree must possess for incorporation in a tree improvement program if the final product is known. Selection criteria for trees destined for pulp differ in some ways from those for trees destined to become veneer. Epicormic branches would be of no consequence in selecting for rapid juvenile growth when trees will be coppiced at very short rotations, as suggested by McAlpine and Brown (1967). Unless otherwise stated, the remarks here will be confined to tree selection where the final product is assumed to be quality lumber for use in furniture or other products where a premium is placed on freedom from defect.

Epicormic branches have been a problem as long as foresters have been managing hardwoods. Many generalities have been made concerning why they arise and what can be done to minimize their occurrence. The fact remains, however, that we still do not understand the basic causes of their eruption. Many silvicultural manipulations intended to control epicormic branches at an acceptable level in natural stands are of limited value. These methods will become less valuable in the future. Why is this so? Simply because if we plan to raise genetically improved trees in the time permissible under prevailing economic conditions, we will have to utilize plantations where intensive practices are applied. Conditions in these plantings seem to be ideal for the eruption of epicormic branches.

Currently, one of the many criteria for selecting hardwood plus trees is that they have no epicormic branches. Even if the only criterion for plus tree selection was resistance to epicormic branching, we would still have difficulty selecting for this trait. This is true for three rather diverse reasons. First, we do not understand the mode of inheritance of epicormic branches. Second, we do not understand the mode of development of epicormics. Third, we are sampling at a given period in time when the selection is made, and this presupposes a status quo pattern for epicormic branch development. Evidence, however, points instead to a dynamic or constantly changing pattern which seems to be strongly influenced by tree age and size and by the effect of environmental factors that may partially or completely mask the individual tree's genetic constitution.

Epicormic branches come in two distinct sizes--long shoots and short shoots. All foresters know that the typical epicormic branches we learned about in hardwood silviculture occur as long shoots. These may occur on the boles after tree damage or stand disturbance. However, in many species the more typical expression of epicormic branching in closed stands is the occurrence of short shoots (fig. 1). Size alone is not the important

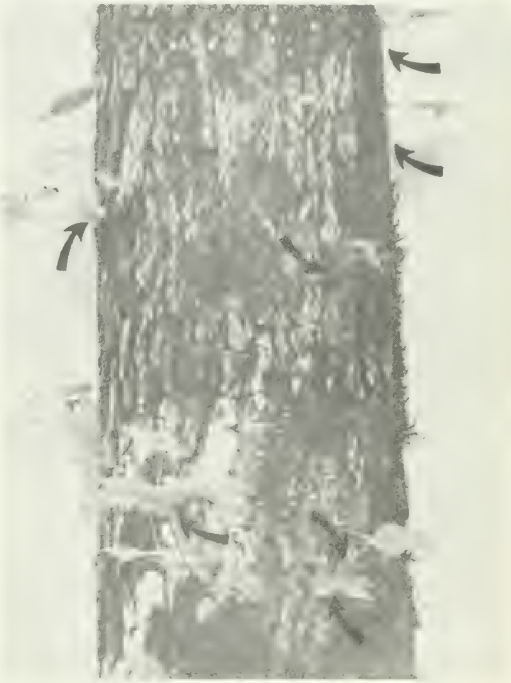

Figure 1. --Short shoots are the typical morphological expression of epicormic branches in undisturbed sweetgum stands. Longer short shoots on left side of bole illustrate environmental effect on short shoot growth habit.

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criterion for classification. The primary consideration is the amount of internodal elongation and short shoots may exist for a number of years as a stalk several inches long or be almost stalkless. In either case, they are transient in nature.

On sweetgum trees, it is not at all uncommon to find a single leaf protruding from the bark with the stalk and bud of the short shoot completely covered. In this species, it is frequently difficult to detect the presence of short shoots during the dormant season because the shoot may not be long enough at this time to extend beyond the bark crevices.

In sweetgum, it is tempting to select a "short-shootless" tree as a desirable plus tree candidate. This is especially true with the emphasis placed on a clear butt log; yet, it is this species that best exemplifies the error that can be made when we attempt to make selections at such a point in time. Sweetgum is therefore a good choice of species to discuss when presenting the problem of epicormic branching in plus tree selection.

A close look at the terminal leader of any sweetgum will reveal the ultimate source of epicormic branches in this species. At each node there is one axillary bud accompanied by two collateral accessory buds (fig. 2). These collateral accessory buds are potential producers of epicormic branches. At some nodes, buds of this type are not readily visible. However, histological examination of these nodes always reveals the presence of the axillary bud and the two bud primordia (fig. 3). The axillary buds at one time or another give rise to branches whose longevity may vary considerably. While these axillary branches function, they inhibit the two associated accessory buds. Removal of these branches results in release and growth of the accessory buds. However, natural senescence and death of the branch does not cause a similar release of bud inhibition.

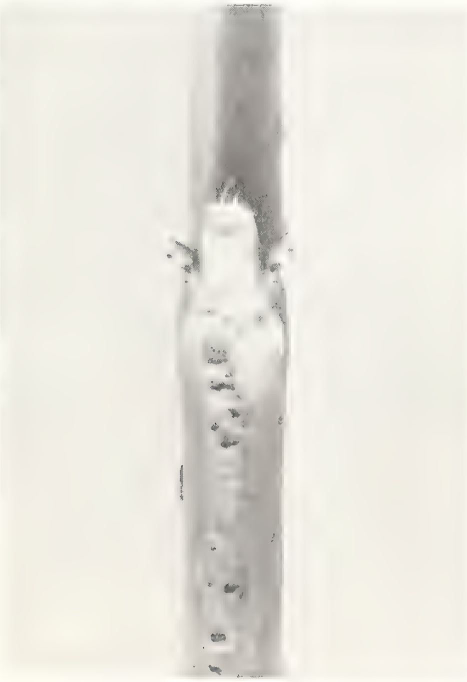

Figure 2.--Each node on the current year's leader of sweetgum characteristically develops two collateral buds which eventually become suppressed trace buds.

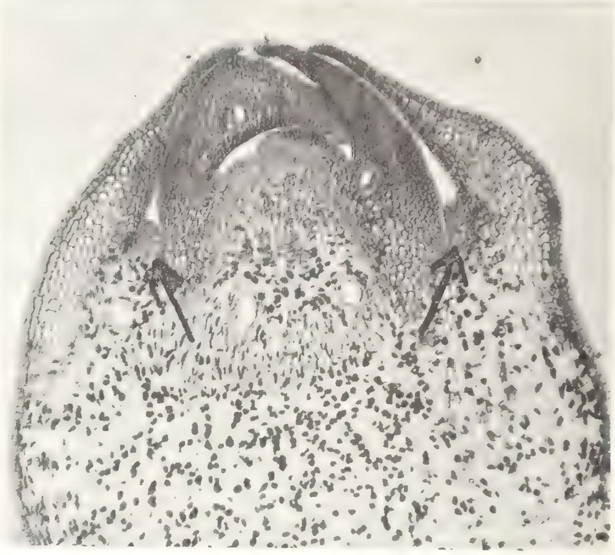

Figure 3.--Even though axillary buds are barely visible at the base of the current year's growth, accessory bud primordia (arrows) are characteristically present. X 100

As the stem increases in diameter during the early life of the tree or shoot, the two accessory buds gradually become embedded in the bark. This usually occurs from three to five years after the buds are initiated. Externally, the accessory buds seem to have aborted, but histological examination reveals that the two well-developed buds are in a transitional stage and only the external scales are being sloughed off (fig. 4). With subsequent radial growth, these buds become completely embedded in the bark. They are now referred to as dormant or suppressed trace buds (fig. 5). The number of potential suppressed buds initiated on the new terminal shoot varies. It is evident, however, that the number is related directly to the number of nodes.

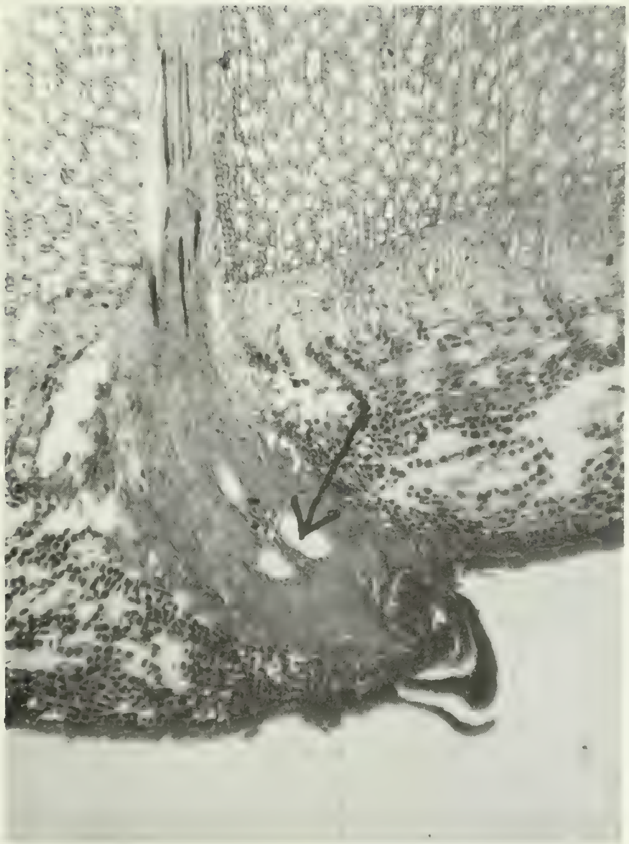

Figure 4.--Accessory buds seem to abort a few years following initiation; however, only the outer bud scales are lost and the bud itself appears to be morphologically unaffected. X 125

The final envelopment of the bud by the bark does not cause complete cessation of growth, as the name suppressed trace bud might imply. On the contrary, these suppressed buds remain physiologically active. It is well known that suppressed buds grow enough to remain outside the expanding ring of wood. But of greater importance to us is that a single suppressed bud can be the progenitor of numerous others (Kormanik and Brown, 1964). This latter phenomenon results in suppressed buds being present in increasingly large numbers as the tree matures. At various times during the life of the tree, suppressed buds are partially released from inhibition and appear as short shoots. This occurs in seemingly random fashion on the bole of the tree, even though the tree has not been damaged or otherwise disturbed. Fortunately, under these conditions the short shoots are short lived, and once established, do not usually develop into long epicormic branches. The point here is that under natural, undisturbed conditions, short shoots rather than long shoots develop. What, then, would happen if the same tree were grown in a plantation at a wider spacing so that short shoots received more sunlight? If all such short shoots elongated as much as four inches and lived for five years, the search for clear lumber would be an extremely difficult undertaking. Depending perhaps on both internal as well as external factors, a poor tree in 1960 may be classified as an excellent tree at present.

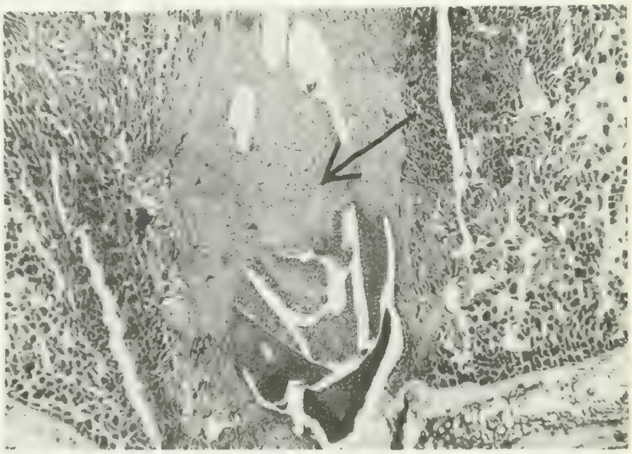

Figure 5.--Suppressed buds such as this one (arrow) are found embedded in the bark of sweetgum of all ages. X 90

Although we have not made long-term observations of short shoot development on individual trees, we have made close examinations of many individual trees over a shorter period of time. A considerable number of mature trees have been cut and the entire boles, from stump to crown, have been sectioned into ½-inch discs to ascertain the presence of suppressed buds. These observations show, first of all, that there may be a period in the tree's development when suppressed buds are prone to multiply. This seems to occur most frequently in the center 8- to 10-inch core. When a stem is within this diameter range, the eruption of a short shoot may be associated with the appearance of additional suppressed buds at the base of each short shoot (fig. 6). We are slowly gathering evidence that this bole area of maximum suppressed bud activity gradually shifts upward as the tree grows, and in time, a clear butt log is evident. Although suppressed buds are present in the butt log, the number of short shoots is greatly reduced. The physiological processes that regulate this apparent change in suppressed bud activity, or degree of inhibition, are

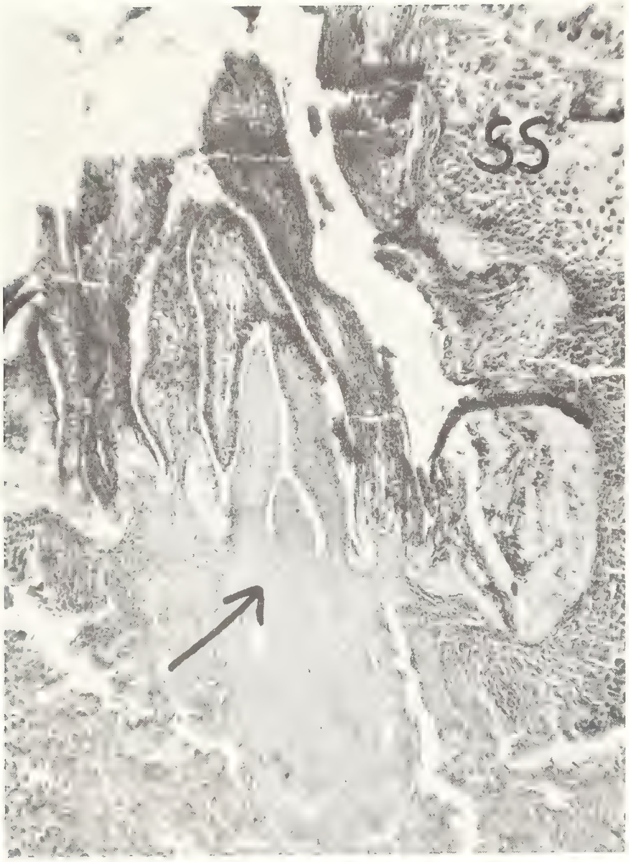

Figure 6.--The development of short shoots (SS) from suppressed buds may result in the proliferation of additional suppressed buds (arrow) that might produce additional short shoots or epicormic branches later in the life of the tree. X 120

poorly understood, as is the role that environment plays in these internal biological processes.

On the terminal leader and for some distance below it as mentioned earlier, the accessory buds, which can become suppressed buds, are inhibited by the action of the associated axillary buds, or, more correctly, by the branches that develop from the axillary. But what factors are involved in inhibition of suppressed buds on older trees after natural pruning has removed the branches low on the bole? Here, apparently, one or more inhibitory processes may be involved. The inhibition can be removed by different stimuli. The mechanisms of inhibition are not known, and in fact may vary among species. Even though our efforts have been concentrated on sweetgum, we feel that we still do not have sufficient developmental information on suppressed buds to search for differences among selected individuals. Furthermore, when one considers the magnitude of the progeny testing job and time involved to do the work, one can reasonably question the value of such an undertaking if it were based on our present knowledge.

During the past several years, we have been placing partial or complete girdles on the boles of trees of several species to determine gross patterns of suppressed bud inhibition. Results have convinced us that suppressed buds are more numerous on most trees than we originally thought. It is not unusual to count 250 epicormic branches and suppressed buds on the first 16-foot log after girdles are placed two or three feet apart along the bole of the tree. Usually, only long shoots are formed as a result of these girdles. Apparently, the girdle completely disrupts the inhibitory process.

Although these studies have shown that suppressed buds are numerous, they have also reinforced our conviction that tree improvement by judicious selection may be possible and indeed practical, for not all individuals of a species produce epicormic branches to the same degree as a result of the girdles. In fact, tree improvement of yellow-poplar may be a relatively simple task. Within this species, about 20 percent of the treated trees fail to produce epicormic branches of any consequence. If after a tree is girdled and released it still produces no epicormic branches, it is unlikely that they will develop at a later time. In fact, when we cut the first log of several such trees into thin discs, we found as few as 5 or 10 suppressed buds, and these had not been stimulated by girdling. However, when we cut several other trees which had sprouted profusely following treatment, we found up to 200 suppressed buds and epicormic branches on the first log.

An extremely interesting pattern of suppressed bud stimulation is becoming apparent through these girdling studies. That is, diffuse-porous species seem to have a different expression in the mechanism of suppressed bud inhibition than do some ring-porous species. However, we will have to treat more ring-porous species before we are certain of this. With diffuse-porous species, a single complete or partial girdle tends to stimulate epicormic branch eruption in a spirally oriented pattern that is quite similar to the tree's natural phyllotaxy. The pattern is, of course, not precise because of the phenomenon of suppressed bud multiplication. The affected area of the bole extends about two feet below the girdle (fig. 7). Usually, below this spiral no additional

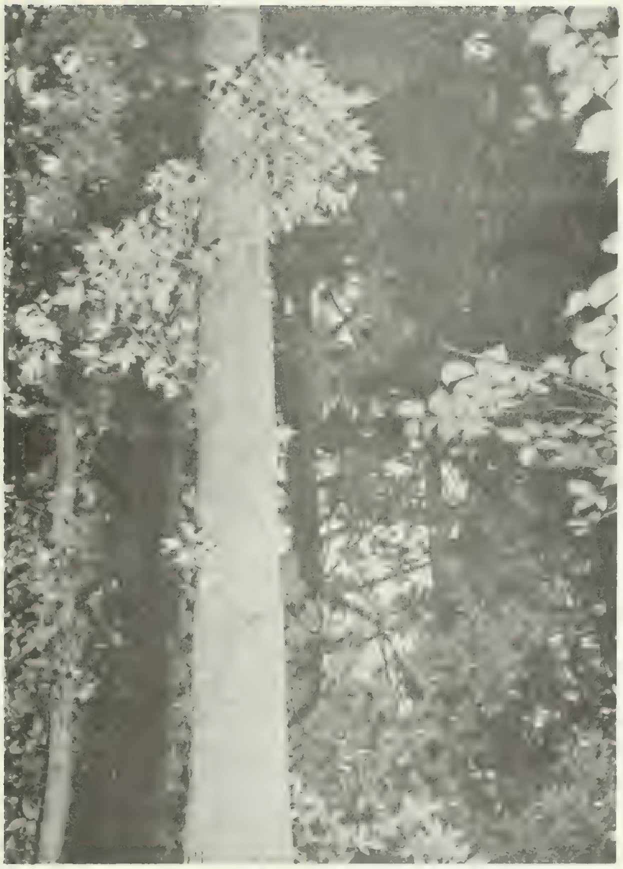

Figure 7.--Eruption of numerous suppressed buds into long epicormic branches following girdling of sweetgum. The epicormic branches show a fairly definite phyllotaxic arrangement, even on old stems.

epicormic branches develop nor are short shoots on the bole visibly stimulated.

With ring-porous oaks, more special problems concerning response to girdling have become glaring. With water oak, on which epicormic branches are frequently found, regardless of stand density, a single girdle results in suppressed bud stimulation from the girdle to the ground. All water oaks girdled exhibited this response, regardless of age or size. White oak sometimes showed the same response as water oak, but frequently failed to respond at all. When we determined the origin of epicormic branches on responsive oaks, we found that at least 30 percent of the epicormics did not have a vascular connection with the pith (Kormanik and Brown, in press 1967). When suppressed white oaks were sectioned, this percentage was much higher. Very few large dominant white oaks produced more than two or three epicormic branches, whereas the suppressed and intermediates produced 30 or more.

In sectioning several large treated white oaks, we found surprisingly few suppressed buds. We have not studied the development of suppressed buds in the oaks and know nothing about any possible developmental patterns. White oak has a reputation for developing epicormic branches; therefore, several things may be happening. Either our three stands of white oaks are completely atypical, or white oak must have a tremendous potential for developing adventitious buds when growing under adverse conditions. Also, suppressed trace buds under these adverse conditions may become quite prolific.

If we cannot look at a tree and determine its tendency towards suppressed bud inhibition, and if we do not as yet have biological procedures for determining physiological differences, what can we do? With our limited knowledge we can only suggest selection criteria for those species which we have studied. For instance, at this stage of the game, the best we can recommend for white oak is to pick strong dominants and give the progeny adequate growing space. For yellow-poplar, response to partial girdling may be an adequate test for resistance to epicormics. Although we are not prepared to set epicormic branch selection guides even for sweetgum, we are convinced that for a rotation of 45 to 50 years, trees between 20 and 30 years of age should be selected, and these should be given complete release before the final determination is made. If selection of trees, based on our present knowledge, is made for sweetgum over age 60, one might be better off to ignore epicormic branching entirely. With this species, it can be emphasized that the lack of short shoots on older trees, even two logs up, should not be construed to mean lack of suppressed buds or superiority in maintaining them in a suppressed condition.

When one considers the fundamental development of epicormic branches, without considering the possibility of inherent differences of suppressed bud inhibition, the possibilities for selective improvement seem bleak. But in reality, inherent differences do exist. It is left to us only to determine methods of ascertaining these differences. Of the species we have examined, green ash perhaps offers us the greatest reason for hope. It is only under most adverse conditions that any but the suppressed and a few intermediate trees develop epicormic branches. The dominants and codominants remain clear. Yet, partial girdles put on dominant and codominant trees produce the most vigorous epicormic branches we have ever stimulated. It is difficult to believe the ability to keep suppressed buds inhibited evolved only in green ash.

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Tubed Seedlings: A Technique for Planting Improved Stock

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Poor survival and initial height growth of certain seedling species like longleaf pine, black walnut, oak, and some others, are major problems. The ability of longleaf pine to become established on dry sand ridges, where few other species are able to survive, suggests that initial root habit of the species is important to survival. Root development and extension are rapid after the seed germinate and seedling roots may penetrate eight feet or more in 10 or 11 months (Wahlenberg, 1946). Derr (1948) found that the survival of 200 longleaf pine seedlings was closely related to the amount of lateral roots broken off in lifting from nursery beds. Height growth after six years for trees with laterals was 4.5 feet and without laterals it was 1.7 feet.

Handling of black walnut seedlings poses a problem. If the taproot is severed during lifting, rot causing fungi may enter the wound causing seedling stunting and mortality. Seedlings are generally large and difficult to handle. Height growth the first year after planting is negligible and seedlings often suffer dieback.

Studies have shown that survival and height growth of red oak and white oak seedlings are often unsuccessful (Williams, 1963). Second-year height growth of red oak ranged from 0.0 to 0.26-foot, and survival ranged from 74 to 86 percent. Seed were planted as part of the study and they grew almost twice as much in height as the transplanted seedlings.

Many nursery grown seedlings with a large root system die as a result of heavy root pruning during lifting because the root systems are not able to meet the water demand of the seedling after transplanting; consequently, the seedling suffers dieback or succumbs. Efforts to lessen the problem by direct-seeding some of the large-seeded and deep-rooted species have not been satisfactory because no repellents are yet available to keep rodents from eating seed such as acorns and walnuts.

Due to the root growth habits of many species it was conceivable that a tube-type container could be developed and used to good advantage. The idea was to plant seed in tubes, let the seedling grow several weeks, and then plant the tubed seedling. We have done some work with tubed longleaf seedlings using different kinds of tubes. The best tubes we have found thus far for this purpose are those made with kraft paper and a non-toxic water resistant glue. Two companies that specialize in making tubes or cores made some special tubes for our study.[3] We also used a polyethylene tube which another company made up for this purpose.

On April 22, 1966, tubes were filled with a mixture of perlite, peat, sand, and soil and then a seed was placed in each tube. About eight weeks later we planted the tubling in a Lakeland loamy sand in south Georgia. Treatments were:

A. Kraft paper tubes, 1-inch i.d. x 10 inches long.
B. Kraft paper tubes, 1½ inches i.d. x 10 inches long.
C. Polyethylene tubes, 7/8-inch i.d. x 10 inches long, solid.
D. Polyethylene tubes, 7/8-inch i.d. x 10 inches long, with two 8-inch slits.
E. Polyethylene tubes, 7/8-inch i.d. x 10 inches long, with twelve 1/4-inch holes.

*A special planting tool was made to plant them.

The seed germinated and the roots of the resulting seedlings grew 10 inches within a 5-week period. In December 1966, six months after planting, survival ranged from 52 percent in polyethylene tubes with holes to 92 percent in 1-inch kraft tubes (table 1). Some of the tubes and seedlings were dug up with as much of the root as possible and most of the taproots were over two or three feet long.

The kraft tubes decomposed rapidly after planting. Root growth was hampered little, and some of the lateral roots went through the wall of the kraft tubes.

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[1] Director, Eastern Tree Seed Laboratory, operated in cooperation with Southeastern Area, State and Private Forestry, and the Southeastern Forest Experiment Station, U. S. Forest Service; Georgia Forestry Commission and Georgia Forest Research Council.

[2] Professor of Forestry and Botany, University of Georgia.

[3] One-inch tubes made by Sonoco Products Co., Hartsville, S. C.; 1½-inch tubes made by Textile Paper Products Company, Cedartown, Ga.

The good survival in the kraft tubes is probably due in part to the uninterrupted root growth which permitted the taproot to continue rapid downward growth and reach moisture. If planting is delayed more than two to three months, this rapid taproot growth may be hampered.

Based on the results of these studies, it appears that a kraft paper tube made with a water resistant, non-toxic adhesive is an excellent carrier for longleaf pine, oak, walnut, and other deep-rooted seedlings.

Table 1.--Average survival of two-month-old tubed longleaf seedlings planted June 15.

Tube Description	Survival percentage	
	August	December
Kraft, 1-inch i.d.	92	92
Kraft, 1-½-inch i.d.	95	88
Polyethylene, solid	84	84
Polyethylene, slit	79	67
Polyethylene, holes	61	52

Due to the persistency of the polyethylene and possible hindrance to root growth, the polyethylene tube cannot be recommended until further results are obtained.

The growing of seedlings in tubes and planting soon after root growth begins offer many advantages, especially in tree improvement work where you want as much uniformity as possible in growing and transplanting seedlings.

ADVANTAGES ASSOCIATED WITH PLANTING TUBED SEEDLINGS

1. The tube method permits the young seedling to begin and maintain rapid root growth in a near natural condition.
2. The V-shaped and L-shaped root caused by planting would not be a problem.
3. One could better schedule seeding and planting to coincide with the species ecology.
4. If demands exceed seedling supply, the tube method would offer a solution since only a few weeks are required from time seed are planted until seedlings are ready to plant.
5. Tubed seedlings offer an opportunity for planting during most of the year.
6. A nursery is not needed; therefore, seedling production could be on a local basis. Expenditures for nursery equipment and facilities are not needed.
7. The tube offers a good potential for mechanization in production of seedlings and in planting of the tublings.
8. Initial seedling development and growth may be improved by the use of special mixed media and fertilizer in the tubes. The addition of systemic pesticides is a possibility.
9. Another advantage of tublings is in studies where 100 percent survival is required. Tubed seedlings in excess of immediate study needs could be prepared and used for replants if some of the original plants died.
10. If seedlings need to be marked, a flag or a marker can be placed in the tube prior to planting.

DISADVANTAGES OF PLANTING TUBED SEEDLINGS

1. The major disadvantage to the tubes at the present time is their cost. Quotations have been $0.013 to almost $0.03 each, depending on size and amount. This cost may be offset somewhat by mechanization, increased survival and improved growth. Cost would be easily justified, however, in research studies.
2. Another disadvantage is transportation and handling of the tubes and tubed seedlings. Until a planting machine is developed and used, planting may be slower than the planting of bare-root stock.

PRECAUTIONS REQUIRED FOR SUCCESSFUL USE OF TUBED SEEDLINGS

1. When ordering tubes, one should be sure to specify that they be made with a water resistant glue and that the glue be non-toxic to plants. Also, the paper should be of a fairly good quality.
2. The tube should be almost completely filled with the medium, with the seed placed on top and lightly covered. The medium should be placed in the tubes in such a way that it will not settle to cause the seedling to be recessed in the tube more than ½-inch.
3. During and immediately after germination, seedlings may need general control measures for damping-off fungi, such as **Fusarium** spp.
4. The seedlings should be outplanted as soon as, or just prior to, the taproot reaching the end of the tube; otherwise, some of the advantage of the tubed seedling may not be realized because taproot growth may be disturbed or lost at planting time.
5. When planted, the tube should be flush with the ground line. If the tube protrudes above the ground line, it may act as a wick and cause a dry condition around the newly planted seedling roots.

6. Avoid planting on sites after extensive site preparation until the soil has settled.

The use of tubes can be a valuable aid in artificial regeneration, especially in the regeneration of our more important and improved hardwoods.

Tubes could also be used in rooting of cuttings. After root initiation, the cutting and tube could be planted without disturbance to the root as is the case when lifted from a rooting bed.

A Study of Racial Variation in Loblolly Pine in Georgia--Tenth-Year Results

JOHN F. KRAUS[1]

The Georgia Loblolly Pine Racial Variation Study was designed to complement the Southwide Pine Seed Source study[2] by testing samples of loblolly pine seed, from collections made in all provinces of Georgia, in plantations established throughout the state.[3] It has performed this function in a most admirable fashion. In general, the results do not conflict in any way with those recently reported on the tenth-year results of the loblolly phase of the Southwide Pine Seed Source Study (Wells and Wakeley, 1966). Basically, the data obtained in the Georgia study indicate that the variation in the growth of loblolly pine from different parts of the state is of sufficient magnitude that it will require consideration in seed procurement and planting plans. It is an important factor in the seed orchard program of the Georgia Forestry Commission.

STUDY DESCRIPTION AND HISTORY

In the fall of 1954, cones were collected from between 20 and 26 trees in each of 14 collection areas in Georgia (figure 1). One collection was made from each of six Georgia Forestry Commission forestry districts, and two collections were made from the remaining four forestry districts. In addition to the 14 collections from Georgia, three lots were obtained from north Florida and one from Arkansas table 1).

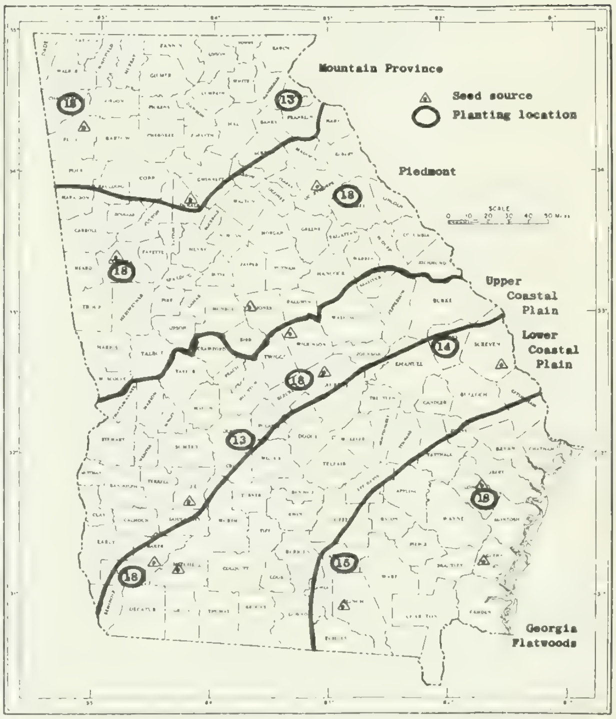

Figure 1. Location of 14 loblolly pine seed sources and 10 planting locations in Georgia. (ⓝ= number of seed sources in plantation)

In the spring of 1955, the seed were sown in the Georgia Forestry Commission's Davisboro Nursery in a randomized block design with two replications. The seedlings were machine lifted in December 1955; bundles made up by plot, block, and plantation; and all necessary stock, including border-row seedlings, were shipped to the cooperators.

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[2] The Southwide Pine Seed Source Study is a cooperative study of the geographic variation of the four major southern pines sponsored by the Committee on Southern Forest Tree Improvement.

[3] Cooperators in this study are: the Georgia Forestry Commission, Union Camp Corporation, Georgia Kraft Company, International Paper Company, Georgia National Forests, Champion Papers Incorporated, and the Georgia Forest Research Council.

Table 1.--Sources of 18 loblolly pine seed lots used in the Georgia Study

PROVINCE	COUNTY	NEAREST TOWN
Mountain	Floyd	Shannon
"	DeKalb	Stone Mountain
Piedmont	Oglethorpe	Lexington
"	Coweta	Newnan
"	Jones	Wayside
Upper Coastal Plain	Wilkinson	Gordon
"	Laurens	Dublin
"	Lee	Leesburg
Lower Coastal Plain	Screven	Halcyondale
"	Baker	Newton
"	Mitchell	Cotton
Flatwoods	Clinch	Homerville
"	Long	Walthourville
"	Glynn	Waynesville
Florida	Baker	Taylor
"	St. Johns	Palm Valley
"	Walton	DeFuniak Springs
Arkansas	Ashley	Crossett

Plantations were established at 10 locations. They were as uniformly distributed throughout the state as the availability of cooperators made possible (figure 1). All 18 seed sources were used at six of the plantations. Due to shortages in planting stock, two plantations contained only 13 sources while the other two each contained 14 and 15 sources. The three north Florida seed sources were planted in both of the Piedmont plantations but only at one location in each of the other four physiographic provinces.

A randomized complete block design was used with four replications of 36-tree-square plots planted at a spacing of 10 x 10 feet. A two-row border strip of commercial stock was planted around all outside boundaries.

With one exception, all the plantations have been remarkably free of damage by fire or man. The plantation in Long County sustained some cattle damage during the first few years, and two corner plots were damaged by site-preparation equipment. Even in these plots, however, sufficient trees remained to permit measurement of heights and fusiform rust (**Cronartium fusiforme** Hedgc. & Hunt ex Cumm.) infection.

During the winter of 1965-66, when the trees were 11 years old from seed, measurements were taken at all plantations of the 16 trees in the center of each plot. Survival, total height, d.b.h., and the incidence of fusiform rust stem cankers and branch galls were recorded on IBM Mark Sense Cards. These cards were processed in the facilities of the Georgia Forestry Commission, and all analyses have been made on plantation-seed source means.

Cubic-foot volume growth was calculated on an individual tree basis using the formula for a cone having a height equal to the plot mean total height and a basal area equal to that at breast height. This value was also used to estimate volume production on a per acre basis in which survival was also a variable.

ANALYSIS AND RESULTS

The principle analysis used combined the data from all plantations for the 14 Georgia seed sources (table 2). In this analysis the state was divided into five physiographic provinces, each containing two plantations (figure 1). The four southern provinces were sampled by three seed sources, while the mountain province was sampled by two.

For each trait, the average values by seed source province and planting province are summarized in table 3. For example, the entry under the piedmont seed source province for the Georgia flatwoods planting province is the mean of six values (three piedmont seed sources planted in two Georgia flatwoods locations). All tests of statistical significance were at the .01 level because there were no comparisons that differed only at the .05 level.

DIFFERENCES AMONG PLANTING PROVINCES

There were no statistically significant differences among the five provinces for any of the traits examined with respect to the overall performance of the Georgia seed sources. Despite the lack of statistical significance, there were two noticeable tendencies. Rust infection and mortality were lowest in the mountain province, and as a consequence, volume production was highest in that area (table 4). In the piedmont, volume growth excelled that of the other provinces as a result of that province producing trees with the best average heights and diameters (table 4). Whether these tendencies are meaningful can best be judged on the basis of the results which follow.

Table 2.--Analysis of variance and mean squares for tenth-year survival, fusiform rust infection height, d.b.h., volume growth and volume production

Source of variation	Degrees of freedom	Mean squares						E(MS)
		Survival	Rust infection	Height	D.b.h.	Volume growth	Volume production	
Planting province A	4	1,342.64	7,257.31	164.20	6.66	6.21	541,980	$\sigma_e^2 + 2\sigma_{as(b)}^2 + 14\sigma_{l(a)}^2 + 28\theta_a^2$
Locations in province L(A)	5	1,092.22**	1,908.22**	51.48**	3.08**	2.38**	150,842**	$\sigma_e^2 + 14\sigma_{l(a)}^2$
Seed source province B	4	613.25**	143.31	48.93**	1.67**	1.73**	9,911	$\sigma_e^2 + 2.8\sigma_{bl(a)}^2 + 10\sigma_{s(b)}^2 + 30\theta_b^2$
Seed sources in province S(B)	9	107.77**	263.45**	1.84	0.21	0.11	11,706	$\sigma_e^2 + 10\sigma_{s(b)}^2$
A x B	16	55.80	25.14	16.00**	0.41**	0.46**	57,266**	$\sigma_e^2 + 2\sigma_{as(b)}^2 + 2.8\sigma_{bl(a)}^2 + 5.6\theta_{ab}^2$
A x S(B)	36	28.33	30.93	1.90	0.12	0.08	7,029	$\sigma_e^2 + 2\sigma_{as(b)}^2$
B x L(A)	20	26.91	53.99	1.71	0.08	0.08	7,849	$\sigma_e^2 + 2.8\sigma_{bl(a)}^2$
S(B) x L(A)	45	25.24	40.74	2.29	0.11	0.07	9,434	σ_e^2

**Significant at the 0.01 level.

DIFFERENCES BETWEEN PLANTING LOCATIONS WITHIN PROVINCES

Within each of the major physiographic provinces, there were plantations at two locations (figure 1). There were highly significant differences between these plantations for all traits, indicating that site, planting procedure, and other local factors were more important than the location of the plantation. Only in the case of rust infection do the data seem to warrant qualification since, despite the lack of statistically significant differences between provinces, rust infection was much lower in both plantations in the mountains. It appears that only the large variation between plantations in the other provinces prevented this difference being significant. The incidence of rust in the most heavily infected of the two mountain locations (Stephens County) was only 12 percent, compared to 42 percent in the next least infected plantation (Dooly County), located in the upper coastal plain.

DIFFERENCES AMONG SEED SOURCE PROVINCES

There were highly significant differences among the five provinces as seed source in survival, height, diameter, and volume growth (table 2). Although the magnitude of these differences was not large for all traits, their trends were rather consistent.

Survival averaged over all plantations was highest for the mountain seed sources (80 percent) and got progressively poorer for each of the southern provinces, averaging 62 percent for the sources from the Georgia flatwoods.

The trend was reversed for height, diameter, and volume growth. The best performance for these traits was attained by trees from the Georgia flatwoods sources and tended to decrease in each succeedingly more northerly province (table 5).

There was a slight tendency for rust infection to be lowest among trees from the mountain seed sources and highest among trees from sources in the Georgia flatwoods, but the differences were neither large enough nor the trend consistent enough to attain statistical significance.

Although it was not included in the analysis of the combined data from the Georgia sources, the performance of the single source from Arkansas was interesting. Trees from this source were unexcelled in survival and resistance to rust infection (table 5). Their exceptional rust resistance throughout the state reinforces previous reports of the low susceptibility to fusiform rust infection of the western sources of loblolly pine (Wakely, 1944, 1961; Bethune and Roth, 1960; Wells, 1966; Wells and Wakeley, 1966). In height, diameter, and volume growth they were intermediate of trees from the piedmont and mountain sources. Due to its high survival and rust resistance, this source produced the highest volumes per acre in all but the mountain and flatwoods provinces (table 3).

The performance of the three north Florida sources is difficult to evaluate since in three of the four provinces in which they were only planted at one location, that location had the poorer average growth for all seed sources. Several correction fac-

Table 3.--Average performance of loblolly pine seed lots grouped by seed source provinces and planting provinces

	Seed Source Province						
Planting Province	Florida[1]	Georgia Flatwoods	Lower Coastal Plain	Upper Coastal Plain	Piedmont	Mountain	Arkansas
				Survival-percent			
Georgia Flatwoods	38.8	59.4	67.3	74.6	72.6	71.5	84.7
Lower Coastal Plain	59.8	60.7	65.3	69.7	66.9	78.1	85.7
Upper Coastal Plain	53.2	66.5	68.0	67.2	75.4	82.5	95.1
Piedmont	46.5	48.1	48.6	59.2	72.5	74.1	77.9
Mountain	79.7	76.5	82.1	87.9	96.2	91.8	98.8
				Fusiform rust infection-percent			
Georgia Flatwoods	90.2	67.6	61.3	63.3	63.6	51.0	14.2
Lower Coastal Plain	92.0	76.5	72.4	73.1	72.5	68.6	21.1
Upper Coastal Plain	89.0	68.0	64.6	62.1	68.2	59.3	9.4
Piedmont	83.1	76.5	59.1	59.6	61.3	62.6	7.8
Mountain	23.3	12.6	9.2	12.6	8.6	8.8	0.1
				Height-feet			
Georgia Flatwoods	26.9	33.3	30.2	29.9	26.8	24.4	28.0
Lower Coastal Plain	31.8	33.3	32.0	31.2	28.2	28.2	29.7
Upper Coastal Plain	26.4	26.0	26.1	26.3	24.9	23.9	25.2
Piedmont	32.8	33.2	32.0	32.9	30.5	30.4	31.2
Mountain	28.4	28.6	29.6	30.7	32.1	30.3	28.6
				D.B.H.-inches			
Georgia Flatwoods	5.6	6.4	5.7	5.7	5.3	4.7	5.4
Lower Coastal Plain	6.4	6.6	6.5	6.2	5.9	5.8	6.1
Upper Coastal Plain	6.1	5.6	5.7	5.7	5.4	5.2	5.2
Piedmont	6.8	7.0	7.0	6.8	6.4	6.4	6.3
Mountain	5.9	6.1	6.2	6.2	6.4	6.3	6.0
				Volume growth-cubic feet			
Georgia Flatwoods	1.74	2.60	1.92	1.82	1.46	1.10	1.52
Lower Coastal Plain	2.42	2.68	2.47	2.22	1.83	1.75	1.99
Upper Coastal Plain	1.78	1.50	1.55	1.61	1.35	1.19	1.26
Piedmont	2.78	2.96	2.96	2.97	2.30	2.26	2.30
Mountain	1.80	1.96	2.10	2.20	2.43	2.17	1.87
				Volume production-cubic feet/acre			
Georgia Flatwoods	307	676	574	584	473	331	532
Lower Coastal Plain	608	678	681	655	515	582	730
Upper Coastal Plain	400	420	420	444	374	395	508
Piedmont	531	566	600	630	690	712	744
Mountain	626	627	739	798	986	817	791

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[1] The three Florida sources are represented in both Piedmont plantings but in only one plantation in each of the other provinces.

tors were tried on these data to see if they might better fit the growth trends established by the Georgia sources. Since the corrected values did not change the relative values appreciably, they have been left uncorrected in tables 3 and 5, and in figure 2. In general, trees from the Florida sources grew slightly slower than trees from sources in the Georgia flatwoods and coastal plain, and sustained slightly higher mortality and rust infection.

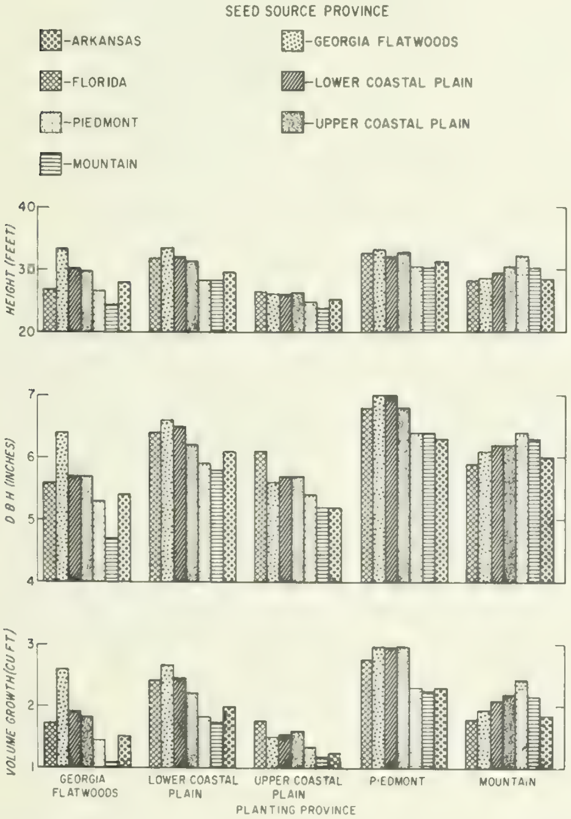

Figure 2 - **Average height, d.b.h., and volume growth of loblolly pine from seven source provinces planted in five Georgia provinces.**

SEED SOURCE DIFFERENCES WITHIN PROVINCES

There were highly significant differences between seed sources within the five major seed collecting provinces in only two traits, survival and rust infection. In the case of survival it is probably best not to place too much weight on these results. Two factors suggesting this interpretation are: (1) the fact that in the Georgia study the seed source with the poorest average survival was not poorest at all locations nor was the best source best at all locations, and (2) too large a portion of the variation in survival may be associated with nursery environment and outplanting procedures.

Differences in rust infection among seed sources were probably less influenced by external factors in this study. The results show that detectable genetic differences exist between specific seed sources in Georgia. These differences are randomly distributed rather than being strongly associated with the major seed source provinces. On the basis of other studies it is entirely possible that a portion of the variation among seed sources is due to the variation between families sampled at each seed source (Barber, 1966).

The least infected seed source in this study consistently had the lowest infection at all planting locations. However, the converse was not true with respect to the most heavily infected source.

THE INTERACTION BETWEEN PLANTING PROVINCE AND SEED SOURCE PROVINCE

The interaction between planting province and seed source province was highly significant for height, diameter, volume growth, and volume production. This interaction is most noticeable in the poor performance of trees from the piedmont and mountain sources when planted in the flatwoods and coastal plain provinces, and the relatively good performance of trees from the flatwoods and coastal plain sources everywhere except in the mountains (table 3, figure 2).

In the Georgia flatwoods the average growth of the local seed sources was noticeably superior to all the non-local sources. When only the Georgia seed sources are considered, trees from the local sources produced the highest volumes per acre in all but the piedmont and mountain provinces (table 3).

GENERAL PERFORMANCE OF THE SEED SOURCES

If the average performance over all locations of the trees from the various sources is plotted on a map at their point of origin, a general trend develops. This trend is shown for height, d. b. h., and volume growth in figure 3, where the average values for the 14 Georgia seed sources are plotted along a transect running from the northwestern corner of Georgia southeast to the Atlantic coast at the southern corner of Camden County. This transect was chosen in preference to a straight north-south line because it comes closer to being at a right angle to a number of biologically important variables, such as physiographic province, altitude, average January temperature, the average number of days without a killing frost, and the average warm season precipitation. The general trend along this transect is definitely clinal, with the values for all growth components increasing from northwest to southeast across the state. There is a slight tendency for this cline to be "stepped" as it crosses the fall line, with generally higher values below the fall line than above it.

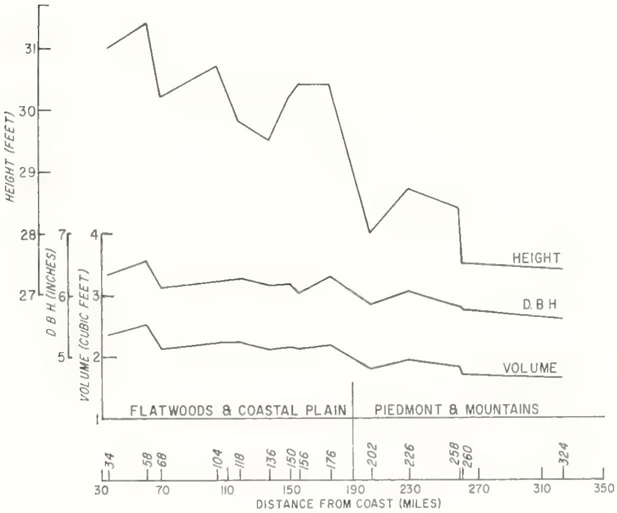

Figure 3 - Trend along a SE-NW transect of growth of 14 Georgia seed sources averaged over 10 plantations.

DISCUSSION

To the forest manager, these results may at first present a dilemma; that is, the fast growing trees from the southern sources are generally less adaptable from the standpoint of initial survival and fusiform rust resistance than the slower growing northern sources. Stand density, however, is one of the more easily controlled factors in plantation management, and given a seed source with with good growth characteristics, it would take only a slightly closer initial spacing to assure a productive, well-stocked stand. Conversely, given a seed source with known good resistance to fusiform rust, many foresters might wish to give serious consideration to a western source, such as that from Arkansas, at the risk of some loss in individual tree performance. Information on total volume yield in relation to specific gravity of wood may be obtained later.

From the standpoint of height, diameter, and individual tree volume growth, the results of the Georgia study clearly show that as far north as the upper coastal plain either the local source or one from the south would be preferable. In the piedmont, trees from the southern sources also grew best and should out-yield the local sources if adequate initial survival is obtained.

In the mountain province, trees from the local sources were inferior in all traits to those from the piedmont, but were generally superior, or nearly equal, to any source from below the fall line.

In the Southwide Study, growth decreased with

Table 4. -- Average performance (in the five physiographic provinces) of the 14 loblolly pine seed sources from Georgia

Planting Province	Survival	Fusiform rust infection	Height	D.B.H.	Volume growth	Volume production per acre
	percent	percent	feet	inches	cu. ft.	cu. ft.
Georgia Flatwoods	69.0	62.1	29.2	5.6	1.83	542
Lower Coastal Plain	67.6	73.0	30.8	6.2	2.22	625
Upper Coastal Plain	71.3	64.8	24.6	5.6	1.46	412
Piedmont	59.7	64.1	31.9	6.7	2.72	634
Mountains	87.5	10.4	30.3	6.3	2.17	792

Table 5.--Average performance of loblolly pine seed sources from seven geographic areas when planted at 10 locations in Georgia

Seed Source Province	Survival	Fusiform rust infection	Height	D.B.H.	Volume growth	Volume production per acre
	percent	percent	feet	inches	cu. ft.	cu. ft.
Georgia Flatwoods	62.5	59.9	30.9	6.3	2.34	593
Lower Coastal Plain	66.6	52.2	30.0	6.2	2.20	603
Upper Coastal Plain	72.3	53.4	30.2	6.2	2.16	623
Piedmont	78.1	53.6	28.5	5.9	1.87	607
Mountain	80.2	48.7	27.4	5.7	1.69	567
Florida[1]	55.6	75.5	29.3	6.2	2.10	494
Arkansas	88.4	10.5	28.5	5.8	1.79	661

[1] The three Florida sources were only planted at six locations.

increasing distance from the coast and a clinal trend was suggested with a possible, but undetected, discontinuity between the coastal I and inland sources (Wells and Wakeley, 1966). The growth trends shown in the Georgia study are definitely clinal along a northwest-southeast transect. Trees from the two sources closest to the coast showed a noticeable tendency toward faster growth than trees from the other seven coastal plain sources. However, an even more abrupt transition was shown between the average growth rates of trees from sources above and below the fall line.

Wells and Wakeley (1966) suggested that selection pressure from climatic variables has influenced the development of clinal variation in loblolly pine. The results of the Georgia study tend to confirm their hypothesis. The "step" in the clinal trend at the fall line coincides fairly well with a general decrease in warm season precipitation. Several additional factors, which could also be associated with changes in the cline, are the increased topographical and soil variation above the fall line and the possibility of introgression with shortleaf pine (**Pinus echinata** Mill.).

It seems quite possible that, with the relatively more abrupt changes in topography and the greater site variation north of the fall line, the loblolly pine in that region have maintained or developed a higher degree of adaptability to the wide range of sites and competitive situations it encounters. This adaptability may be maintained at the expense of fast growth rates.

On large-scale maps, it can be seen that the intensity of shortleaf pine occurrence increases greatly north of the fall line while it is very scarce, near the Georgia coast, in Livingston Parish, Louisiana, and in Onslow County, North Carolina (Mohr, 1897, Roberts and Cruikshank, 1941; Janssen and Weiland, 1960). Shortleaf pine also attains its its heaviest concentration in southwest Arkansas, very close to the origin of the most fusiform rust resistant trees in the Georgia study. Introgression of shortleaf with loblolly pine in that area has already been suggested to account for the similar low rust infection of the Arkansas and Texas sources in the Southwide Study (Wells and Wakeley, 1966). It may also be associated with the clinal variation in loblolly pine growth rates.

SUMMARY

For a smaller but more intensively sampled area, the tenth-year results of the Georgia Loblolly Racial Variation Study largely substantiate those obtained from the Southwide Pine Seed Source Study. The general conclusions which apply are similar:

1. *Racial variation in loblolly pine in Georgia is clinal, with growth rate decreasing with increasing distance from the coast.*
2. *Within Georgia, trees from provinces south of the planting province grew best in all but the Georgia flatwoods.*
3. *Trees from a western source (Arkansas) had the lowest percentage of rust infection.*

Among the Georgia sources, trees from the northern seed sources survived best.

If the trends shown by these tenth-year data continue in the same relative pattern until rotation age, and pulp yields are satisfactory, they will be of great practical and theoretical significance.

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Fifth-year Results of a Slash Pine Polycross Progeny Test in Georgia [1]

Timothy LaFarge and John F. Kraus[2]

In 1954, seed orchards of selected slash pine (**Pinus elliottii Engelm.**) and loblolly pine (**P. taeda L.**) were established in Georgia by the Georgia Forestry Commission to develop and produce superior seed. Progeny testing of the selected trees was initiated as soon as pollen production and female flowering were sufficiently abundant in the orchards to permit controlled pollinations.

This paper reviews the fifth-year results of the first slash pine progeny test to be outplanted. This planting tests 35 of 179 slash pine clones in phase I of the progeny testing program used by the Georgia Forestry Commission to develop its seed orchards.

Phase I involves controlled pollinations of all slash and loblolly pine clones in the orchards with a mixture of pollen from 15 or more clones in the orchards. Two other phases complete the program. Phase II consists of pollinating 30 clones each of slash and loblolly pine with the pollen of at least five different clones of the relevant species. In phase III those clones used in phase II will be self-pollinated.

The objectives of phase I and of this progeny test are: (1) to estimate, on the basis of several important traits, the general combining ability of each clone; i. e., what the relative performance, or breeding value, of each open-pollinated clone might be when the orchards are at full seed production; (2) to provide a basis for roguing undesirable or relatively inferior clones so that seed certification requirements defined by the Georgia Crop Improvement Association may be met (1965, G.C.I.A. Certification Standards for forest tree seed, pp. 80-84); and, (3) to identify those clones that are exceptional in the most important traits and which are, therefore, preferable for use in further crosses.

These objectives and other considerations have been reviewed in greater detail by Barber (1958)[3] and by Webb and Kraus (1966).

MATERIALS AND METHODS

This test is composed of two contiguous outplantings, plantations 57 and 58. Each plantation contains progenies of 19 clones and one commercial check lot. Three progenies are included in both plantations for purposes of comparison, so that 35 half-sib families are studied.

All clones involved in this test were pollinated in 1958 with a mixture of the pollen of 30 clones from the orchards. This mixture was designated mix I and represented all the clones from which sufficient pollen was available at that time. This procedure was chosen so as to give a good approximation of the pollinations between clones as they might naturally occur in the seed orchards, assuming seed orchard pollen was abundant and contamination from outside sources was insignificant (Barber, 1958).[3]

The seed lots used as the controls in this study were collected from Georgia Forestry Commission forestry districts within the natural range of slash pine in south Georgia. They were intended to represent the general genetic quality of seed being used to establish plantations in Georgia when this study was initiated.

The outplanting is located in Bleckley County, Georgia, on the upper coastal plain. Both plantations were established in January 1961 with 1-0 nursery stock. Each plantation is arranged in a randomized complete-block design with six replications. The trees are planted at an 8.5 x 8.5 foot spacing in 25-tree square plots. Because of an insufficient supply of seedlings of certain progenies in the nursery at the time of planting, there are two missing plots in plantation 57. Plantation 58 is complete.

Measurements

Two of the measurements were executed during the month of November 1965, as follows: (1) total height was determined with a pole graduated to the nearest tenth foot, and (2) the number of stem and branch cankers caused by fusiform rust (**Cronartium fusiforme** Hedgc. and Hunt ex Cumm.) were counted on each tree. These measurements had also been recorded in 1963 after three growing seasons in the field. A third measurement, the crown width/total height ratio, was taken in March 1966 shortly before new growth was initiated. This trait was measured with a transparent plastic board calibrated so as to give the measurements as direct readings in units of ten percent. Since all data for each tree were recorded on IBM Mark-Sense cards, the number of cards per plot gave an automatic tally of survival.

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[1] Cooperators in this study were: the Georgia Forestry Commission, the Continental Can Company, and the Georgia Forest Research Council.

[2] Assistant Silviculturist, and Plant Geneticist, respectively; Southeastern Forest Experiment Station, Forest Service, Macon, Georgia.

[3] Barber, John C. Preliminary work plan for the progeny testing of trees used by Georgia Forestry Commission in the development of seed orchards. Southeastern Forest Experiment Station, Macon, Georgia. 1958. (Unpublished, 18 pp.).

Statistical Methods

Plot means were calculated for all variables, which consisted of: (1) number of trees surviving; (2) total height; (3) crown width/total height ratio; (4) average number of cankers per tree; (5) average number of cankers per infected tree; (6) percentage of trees free of rust; and (7) percentage of trees with stem cankers.

The percentages of trees free of rust and trees with stem cankers were transformed to arcsin $\sqrt{\text{percent}}$. All seven variables were then subjected to analysis of variance, which consisted of the standard F-test of the randomized complete-block design. Simple and partial phenotypic correlation coefficients between some of the variables measuring rust infection were calculated in an attempt to determine which parameter best represented the patterns of rust infection.

Duncan's new multiple range test was used to compare the progenies for total height, the crown width/total height ratio, and the average number of cankers per tree. Finally, regression analysis was used to rank all progenies in both plantations together on the basis of the three common progenies. In this manner, all progenies in both plantations were compared directly with each other and evaluated according to the above three traits.

DISCUSSION OF RESULTS

Fifth-year survival was 93 and 91 percent for plantations 57 and 58, respectively, and the range in each plantation varied from 87 to 97 percent. Because very little variation between progeny lines was indicated for survival (table 1), it was not included in any further analysis.

Analysis of Variance

There were significant differences between progenies for all variables except total height in plantation 57, percentage of rust-free trees in plantation 58, and survival in both plantations (table 1). The percentage of trees with stem cankers was significant at the 5 percent level in plantation 58, but all other differences were highly significant.

Reliability of Earlier Measurements

Data on total height and rate of infection (percentage of rust-free trees) had also been recorded after three years in the field. In order to test the

Table 1. – Summary of F-tests of slash pine progenies in Plantations 57 and 58

Source of variation	Degrees of freedom	Number of trees per plot	Total height	Crown width/ total height ratio	Average No. of cankers per tree	Average No. of cankers per infected tree	Percentage of rust-free trees	Percentage of trees with stem cankers
				Plantation 57				
Block	5	2.72*[1]	7.51**	16.55**	5.69**	4.14**	3.19*	3.34**
Progeny	19	1.01 NS	1.42 NS	4.50**	7.66**	3.58**	13.56**	4.47**
Error	93[2]							
				Plantation 58				
Block	5	0.80 NS	10.37**	0.99 NS	5.56**	4.17**	2.70*	2.61*
Progeny	19	.92 NS	2.28**	9.11**	4.53**	4.47**	1.68 NS	2.05*
Error	95							

[1] * Significant at the 5% level
** Significant at the 1% level.
NS Not significant.

[2] Two degrees of freedom lost due to missing plots.

reliability of the earlier measurements, correlations between the third- and fifth-year data of five variables were calculated (table 2). Although most of the correlations for rust-infection parameters were high in plantation 57, they were low in plantation 58. Such erratic results imply that after three years the overall severity of rust infection may not have been sufficient to give an accurate evaluation of the rust resistance of the progeny lines. It is generally considered that favorable conditions for severe rust infection must be present for an adequate test of resistance to the disease. At five years of age, the probability that all progenies have been thoroughly exposed to infection is much greater. It also may be assumed that after five years most of the infection that may reduce the merchantability of the trees has occurred. Thus, third-year measurements do not seem to be very reliable for determining the relative rust resistance of progeny lines. However, such an estimate of the accuracy of the fifth-year rust infection data must await the tenth-year measurements.

Table 2. – Summary of simple phenotypic correlations between third and fifth year measurements of slash pine progenies in Plantations 57 and 58

Variables compared	Correlation coefficient (r) [1]	
Third year measurements vs. Fifth year measurements	Plantation 57	Plantation 58
Total height	0.871**	0.923**
Average number of cankers/tree	0.594**	0.265 NS
Average number of cankers/infected tree	0.296 NS	–0.301 NS
Percentage of trees free of rust	0.626**	0.390 NS
Percentage of trees with stem cankers	0.611**	0.506*

Selection of Variables

Of the seven variables analyzed, four deal with the degree of rust infection. In an attempt to determine which variable might have the greatest general utility for analyzing inherent disease resistance, several simple phenotypic correlations between three of these parameters were calculated (table 3).

It would seem that these generally high correlation coefficients are to be expected simply because all three variables are expressions of rust

Table 3. – Simple phenotypic correlations between selected variables of slash pine progenies in Plantations 57 and 58

Variables compared	Correlation coefficient (r) [1]	
	Plantation 57	Plantation 58
Average number of cankers per tree vs. average number of cankers per infected tree	0.868**	0.976**
Average number of cankers per tree vs. percentage of trees free of rust	–0.851**	–0.802**
Average number of cankers per infected tree vs. percentage of trees free of rust	–0.486*	–0.686**

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[1] Values which exceed ±0.444 are significant at the 5% level (*). Values which exceed ± 0.561 are significant at the percent level (**).

infection. However, the percentage of trees free of rust and the number of cankers per infected tree are parameters which represent separate subpopulations; i. e., they are unrelated and have different means and variances. Because of this difference in population characteristics, the significant correlation between these two variables is meaningful. That is since this correlation was significant in both plantations and was not confounded with any other effects, it can be interpreted to mean that those progenies with fewer infected trees are more likely to have fewer cankers on the infected trees. Those results are in agreement with findings reported by Goddard and Strickland (1966, p. 11), who found a significant negative correlation ($r = -0.57^{*}$) between the percentage of trees free of rust and the severity of rust on infected slash pine trees (number of cankers per infected tree).

On the other hand, any variation in either the number of uninfected trees or the number of cankers per infected tree will affect the average number of cankers per tree. Also, the relationship of the average number of cankers per tree to each of the other variables is confounded by the fact that they are significantly correlated with each other. For example, it could not be concluded that the relationship between the average number of cankers per tree and the percentage of trees free of rust would be the same if a different set of values for the number of cankers per infected tree were considered.

To clarify these relationships, partial correlation coefficients were calculated such that the average number of cankers per tree was correlated with each variable while the alternate variable was held constant (table 4). These very high partial correlations indicate that in this study the average number of cankers per tree reflected quite accurately both the rate of infection and the severity of attack on each progeny. Also, as shown in table 1, highly significant differences between progenies were obtained for this variable in both plantations. On the basis of these statistics, it seems reasonable to conclude that the average number of cankers per tree is the most useful single variable for evaluating the resistance to rust infection among progeny lines. Therefore, the remaining portion of this discussion is limited to the following three variables: (1) total height; (2) the crown width/total height ratio; and (3) the average number of cankers per tree.

Multiple Range Tests

Generally, progeny performance relative to the controls was very good. In the Duncan's new multiple range test for total height, the control lots ranked poorly in both plantations (figure 1). In plantation 57 three progenies were significantly better at the five percent level than the control, which ranked next to last; in plantation 58 four progenies were significantly higher than the control, which ranked eighteenth.

This trend was even more striking for the crown width/total height ratio (figure 2). In both plantations the controls ranked next to last. In plantation 57, six progenies had significantly narrower crowns than the control, and in plantation 58, seventeen were significantly better.

Table 4. – Partial correlations between selected variables of slash pine progenies in Plantations 57 and 58

Variables compared	Correlation coefficient (r) [1/]	
	Plantation 57	Plantation 58
Average number of cankers per tree vs. average number of cankers per infected tree (percentage of trees free of rust held constant)	0.989**	0.993**
Average number of cankers per tree vs. percentage of trees free of rust (average number of cankers per infected tree held constant)	–0.986**	–0.949**

[1/] Values which exceed ± 0.575 are significant at the 1 percent level (**).

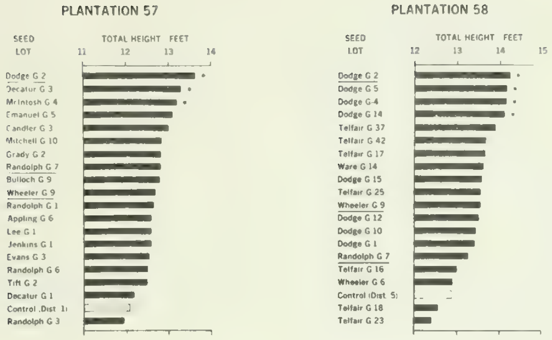

Figure 1 Progeny lines and controls in Plantations 57 and 58 ranked according to total height Underscored progenies are common to both plantations (• indicates progenies significantly taller, at the 5 percent level, than the control)

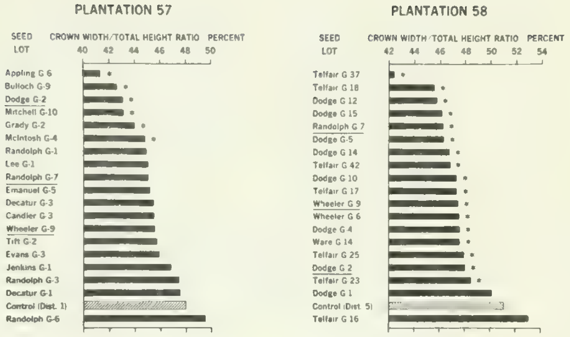

Figure 2 Progeny lines and controls in Plantations 57 and 58 ranked according to the crown width/total height ratio Underscored progenies are common to both plantations (• indicates progenies with significantly narrower crowns, at the 5 percent level, than the control)

Improvement was much less convincing for rust resistance (figure 3). In plantation 57, seven progenies had significantly fewer cankers than the control, but five progenies ranked lower than the control. In plantation 58, only one progeny significantly outperformed the control, which outranked 12 progenies. A more intensive method of selection for rust resistance seems to be needed.

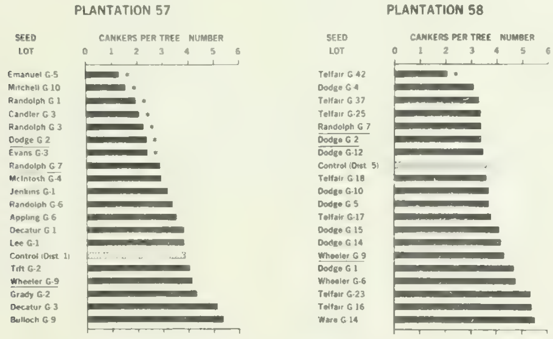

Figure 3 Progeny lines and controls in Plantations 57 and 58 ranked according to the average number of cankers per tree Underscored progenies are common to both plantations (• indicates progenies with significantly fewer cankers per tree, at the 5 percent level than the control)

Evaluation of Progeny Lines

Three progenies are common to both plantations. The relative performances of these progenies in each plantation were used to adjust all progeny lines to a common base so that they could be compared directly with each other. To accomplish this, regressions of the three progeny means for each variable in plantation 58 on their corresponding means in plantation 57 were calculated. The prediction equation for each variable was then used to adjust all progenies in plantation 57 to the same base as those in plantation 58. The correlation coefficient (r) between plantations for each variable was also calculated. None of these correlations were significant, but two of them were high. They were: (1) for total height, r = 0.912; (2) for the average number of cankers per tree, r = 0.942; and (3) for the crown width/total height ratio, r = 0.316 (based on only two common progenies, since Dodge G-2 was so far out of line that it reversed the slope of the regression equation). The required $r_{.05}$ was 0.950. Nevertheless, the use of regression seems justifiable as a practical method of comparing the performances of all lines from both plantations.

To evaluate the progeny lines for all three traits, total height is plotted over the crown width/total height ratio (figure 4) and over the average number of cankers per tree (figure 5). The mean of all progenies for each trait is indicated by horizontal and vertical lines on each graph. In figure 5 a second vertical line denotes a control (District 5). Since the value for this control is superior to the mean number of cankers per tree, it is used instead of the mean to evaluate the progenies for that trait. Thus, all clones whose progenies excelled either

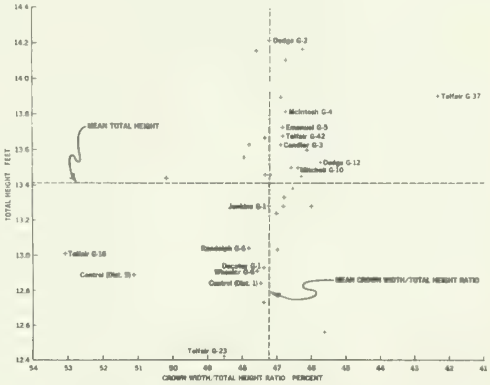

Figure 4 Slash pine progenies ranked according to the relationship of total height vs. the crown width/total height ratio

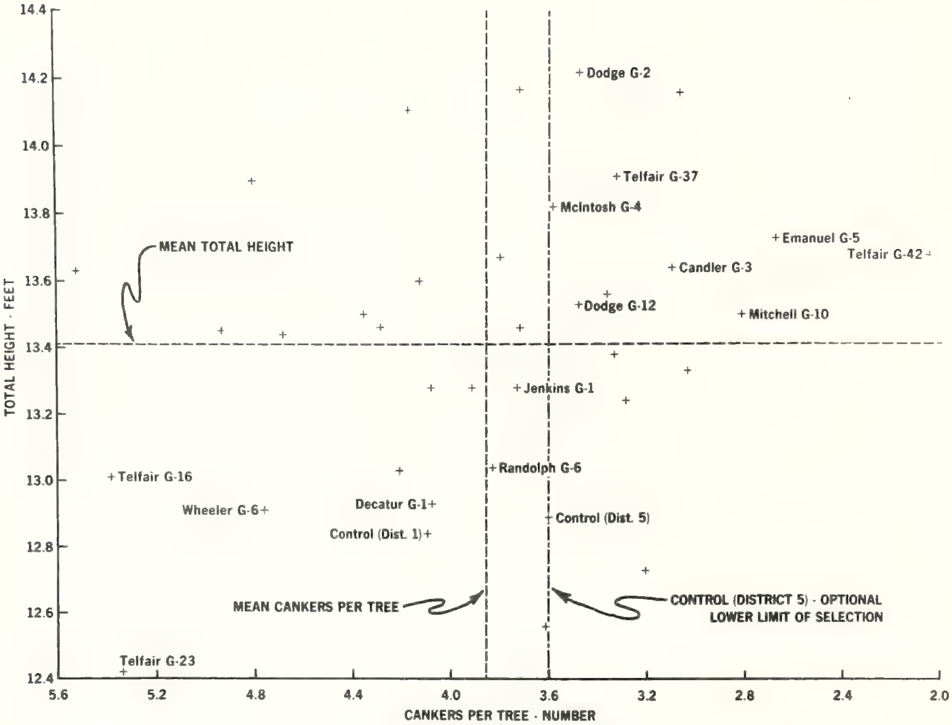

Figure 5. Slash pine progenies ranked according to the relationship of total height vs. the average number of cankers per tree.

the mean or the best control (if the control was better than the mean) for all three traits are considered superior and are therefore recommended for future breeding work. Graphically this means that those progenies which fall in the upper right quadrant of each graph are considered superior and are labelled. Conversely, the clonal parents of those progenies which fall below all three means (the lower left quadrant of each graph) may be considered undesirable and could be culled from the seed orchards if necessary. These are also labelled, but all other progenies are not. Of the total of 35 clones, eight are superior. These are Dodge G-2, Dodge G-12, Telfair G-37, Telfair G-42, McIntosh G-4, Emmanuel G-5, Candler G-3, and Mitchell G-10. It should be noted that most of these "superior" lines performed well when ranked according to the other expressions of rust infection that were also analyzed. On the other hand, there are six progeny lines which are below average in all three traits. These "inferior" progenies are Telfair G-16, Telfair G-23, Jenkins G-1, Randolph G-6, Decatur G-1, and Wheeler G-6.

Actually clones will be rated on many traits such as wood quality, seed production or anything else that may show up in tests and which is important in seed orchard use. Also, results from Phase II and Phase III of the progeny testing program may provide important information useful in culling clones.

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Ninth-Year Performance of Slash and Loblolly Pine Nursery Selections in Georgia [1]

DAVIE L. HUNT [2]

One of the various methods of individual tree selection which has been suggested for use in tree breeding is the selection of outstanding seedlings from nursery beds. It is an intensive selection method because it involves the examination of large numbers of trees. It is also an extensive selection technique because a relatively large number of trees can be selected in a short time. The principle criticism of nursery selection has been the lack of data showing a good correlation of juvenile height growth with mature tree characteristics. The objective of this study was to test the utility of nursery selection, and to provide trees for future applied breeding by selecting seedlings of outstanding vigor from the Georgia Forestry Commission nurseries.

Nursery selections were made for several consecutive years by the Tennessee Valley Authority in loblolly pine (**Pinus taeda L.**), shortleaf pine (**Pinus echinata** Mill.), and eastern white pine (**Pinus strobus L.**) (Ellertsen, 1955, 1957). In all species and age classes, the average height at the end of the 1956 growing season for the super-seedlings was at least 0.7 of a foot taller than the controls.

Zobel, Goddard, and Cech (1957) reported on a loblolly pine nursery selection study conducted by the Texas Forest Service. These selections were from nursery beds where the seed had been graded; within the medium size seed class, three types of selections were made: (1) better than average seedlings; (2) average seedlings; and (3) inferior seedlings. After five growing seasons, the outstanding seedlings were about 25 percent taller than the average seedlings, and the inferior seedlings were about 20 percent shorter than the average selections.

Bengtson (1963) reported from Florida on selections from slash pine (**Pinus elliottii** Engelm.) nursery beds. After 8 years in the field, the select seedlings averaged 23 percent taller than the controls.

STUDY HISTORY

In 1954, approximately 85 million slash pine seedlings and 25 million loblolly pine seedlings were grown in the four Georgia Forestry Commission nurseries. All of the beds in each of the nurseries were examined in November, at the beginning of the lifting season. Seedlings which appeared to be superior in height, diameter, or any other obvious form of outstanding vigor, in relation to the surrounding seedlings, were marked. These candidates were later re-examined and final selections made. When a select seedling was lifted, an average adjacent seedling to be used as a check was lifted and the two tied together. Of the 110 million seedlings examined, 582 slash and 571 loblolly seedlings were selected, which gave a selection ratio of 1:146,000 and 1:44,000, respectively.

The study was planted on sandy upland old fields in Twiggs County in central Georgia. The trees were planted in three separate fields with the paired seedlings planted side by side within the row. Field I contained 25 rows of 28 loblolly seedlings; Field II contained 11 rows of 40 loblolly seedlings; and Field III contained 35 rows of 34 slash seedlings.

At the end of the fourth growing season, the loblolly pine and slash pine select seedlings were 16 and 19 percent taller, respectively, than the controls (Barber and VanHaverbeke, 1961). The select seedlings for both species had a higher average number of fusiform rust (**Cronartium fusiforme** Hedgc. & Hunt ex Cumm.) infections per tree than the controls. This was attributed to the fact that the select trees were larger and had more crown exposed to the fusiform rust infection. Barber and

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[1] Cooperators in this study were the Georgia Forestry Commission, the Georgia Kraft Company, and the Georgia Kraft Company.

[2] Forestry Research Technician, Southeastern Forest Experiment Station, Forest Service, Macon, Georgia.

VanHaverbeke also reported that, except for the loblolly controls, the percentage of rust-free trees in all height classes was similar, indicating that the more vigorous trees were not more susceptible to rust.

In December 1963, after nine growing seasons, the plantations were severely damaged by ice. As a data-salvaging operation, height and diameter at breast height were measured in April 1964. The trees that were broken into one or more pieces were reconstructed and measured, and the trees that were bent over were measured in sections or with a flexible tape. Individual tree volumes (outside bark) were calculated as that of a cone with a height equal to total tree height and a basal area equal to that at breast height. The study was terminated because of the severe ice damage. The plantation will continue to be maintained for the possibility of using some of the trees in a breeding program.

Differences between the select seedlings and their checks at 9 years were compared by t-tests calculated separately for each field. The results showed that the superiority of the select trees over the control trees for height, d.b.h., and cubic-foot volume was highly significant for all fields. The t-value for all tests was significant with 99 percent confidence.

In field 1 (loblolly) 39 percent of the paired trees survived. Among these 135 pairs, the select trees averaged 2.1 feet taller, 0.6 inch larger in d.b.h., and 0.5 cubic foot more volume than the controls (figure 1A). In Field II (loblolly), 39 percent of the paired trees survived. Among these 86 pairs, the select trees averaged 1.7 feet taller, 0.5 inch larger in d.b.h., and 0.4 cubic foot more volume than the controls (figure 1B). In Field III (slash), 41 percent of the paired trees survived. Among these 237 pairs, the select trees averaged 1.6 feet taller, 0.5 inch larger in d.b.h., and 0.4 cubic foot more volume than the controls (figure 1C). Based on the paired trees, the select loblolly and slash trees had 20 and 22 percent more cubic-foot volume, respectively, than the controls.

After four growing seasons, the difference in average height between the select and control trees

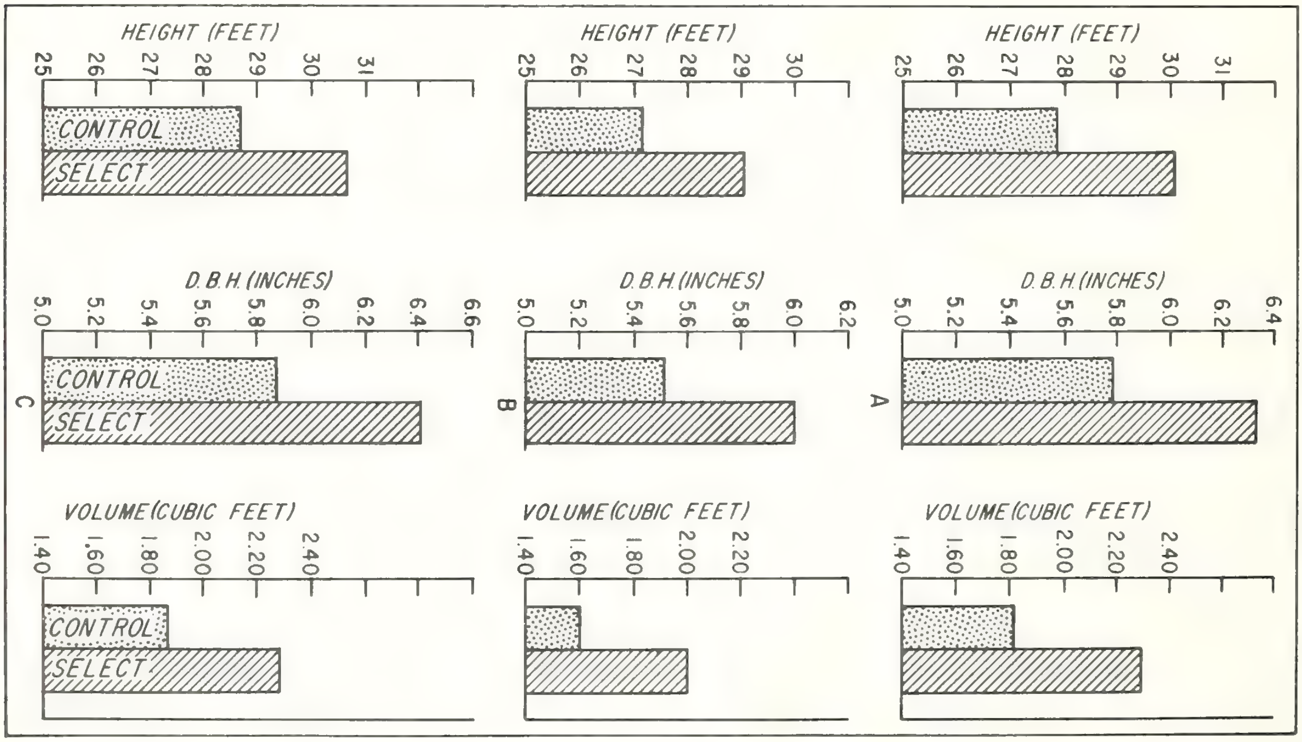

Figure 1.-- The average height, d.b.h., and cubic-foot volume for all paired trees in loblolly pine, Field 1 (A); loblolly pine, Field II (B); and slash pine, Field III (C).

had increased yearly in both species (Barber and VanHaverbeke, 1961). After 9 years, the data show that the select loblolly trees were still increasing their height advantage and averaged 1.9 feet taller than the checks, compared to 1.3 feet at 4 years.

Conversely, the height advantage of the select slash decreased slightly from 1.8 feet at 4 years to 1.6 feet after 9 years.

From observation, some of the selected trees were superior in other qualities, such as crown form and pruning ability. There were also indications that some trees were resistant to fusiform rust because they were uninfected after 9 years, even though the rate of infection in the study as a whole was very high. Not all of the select trees were superior to their paired check trees; in some cases, the controls had above-average qualities.

CONCLUSIONS

The selection of outstanding loblolly and slash pine seedlings in the nursery was shown to be a feasible means of locating trees potentially outstanding in vigor for use in future breeding work. This method of selection could also be considered for the establishment of seed production areas or seedling seed orchards.

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Variability of Chromosome Structure and Behavior in Southern Pine Hybrids [1]

L. C. SAYLOR[2]

INTRODUCTION

Interspecific hybridization is a technique of considerable importance to plant breeders. Although hybridization of forest tree species has not received a great amount of emphasis in the past because of the wealth of species in existence and the intraspecific variability they possess, its importance is becoming more evident as our knowledge and sophistication of tree improvement increase.

The value of incorporating the germplasm of one species into that of another species for such purposes as increasing resistance to insects and diseases is being continually documented. In the southern pines, for example, Grigsby (1959) has demonstrated increased resistance of slash x shortleaf and loblolly x slash (var. **densa**) pine hybrids to **Rhyacionia frustrana.** Derr (1966) has shown similarly that longleaf x slash hybrids appear less susceptible than their parents to the brown spot needle blight of longleaf pine and the fusiform rust of slash pine.

Interspecific hybridization also may provide new combinations that are more tolerant to unusual climatic conditions (Hyun and Ahn, 1959). In an attempt to develop strains with such tolerances, several hybridization projects have been initiated recently in the South to produce trees that can be grown commercially on unproductive sites that are extremely wet or dry.

A very important project for forest geneticists, therefore, is to determine how readily species will cross. For those species that cannot be crossed or that cross only with difficulty, it is also of value to determine the barriers. As Critchfield (1962) pointed out, there are two general types of isolating mechanisms operating in the southern pines, those that prevent cross pollination and those that prevent germination of the seed. Alterations in chromosome structure and genetic make-up are two features of the latter type that may prevent the production of hybrids. They also may cause the hybrids to be infertile once they reach sexual maturity, which causes such trees to be of little or no use for future breeding programs.

The purpose of this project was to study four species of southern pines and their hybrids to determine if chromosome structure and behavior were in any way a barrier to the interspecific exchange of genetic material.

MATERIALS AND METHODS

Staminate cones with pollen mother cells in various stages of division were collected from 35 trees during a three year period from 1961-1963. The material analyzed included three species and ten different hybrid combinations of **P. echinata, P. elliottii** var. **elliottii, P. palustris,** and **P. taeda.** Three of the crosses were combinations involving three species.

Most of the trees studied were located in the Fastrill Arboretum of the Texas Forest Service near Alto, Texas, and in the Hodges Gardens at Hodges, Louisiana. The others were located near Raleigh, North Carolina and near Placerville, California in the Eddy Arboretum of the Institute of Forest Genetics. An attempt was made to obtain material from several hybrids located in the Harrison Experimental Research Forest of the Institute of Forest Genetics at Gulfport, Mississippi, but either the trees were not sexually mature or the pollen mother cells were not dividing at the time the collections were made.

Immediately after collection, the staminate cones were sliced in half longitudinally and fixed in a 3:1 solution of absolute ethyl alcohol and glacial acetic acid. The material was subsequently changed to 70% alcohol and stored in a freezer. The microsporocytes were stained in aceto-carmine for analysis.

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The method of analysis used was similar to that described by Saylor and Smith (1966). Frequencies of meiotic irregularities were determined for each tree in six different stages. Approximately 1500 division figures (250 per stage) were studied for each tree. To facilitate presentation of the data, similar irregularities in the two cycles of division were combined and presented as a single percentage figure.

RESULTS

Chromosome behavior was entirely regular in a vast majority of the cells studied, and this was true for all stages. Irregularities of some type were found, however, for every tree.

Univalents were the most common irregularity observed. Frequencies of greater than one percent were found in 15 trees for this abnormality. Frequencies of the other irregularities exceeded one percent as follows: lagging chromosomes - 7 trees; fragments - 7 trees; bridges - 8 trees; micronuclei - 5 trees.

The results of this study in conjunction with those of other studies, indicate that the hybrids are slightly more irregular than trees representing parental species. For example, 36.7 percent of the hybrids listed in Table I had total irregularity frequencies greater than one percent. For comparison purposes, irregularity frequencies greater than one percent occurred as follows in a natural population study of loblolly and pond pines: loblolly pine - 16.7%, loblolly x pond pine hybrids - 31.8%; pond pine - 16.7%.

Of the different hybrid combinations studied, the **P. echinata** x **taeda** cross was the most irregular. The reason for this is not understood, and it is possible that several factors may be involved. Tree 1 is the female parent of all of the hybrids of this cross (trees 7-10); it is also the female grandparent of hybrids 22, 23 and 31-35. The level of meiotic irregularity observed in tree 1 is greater than normal for pure species, which indicates the possible presence of genetic or chromosomal abberations that could be passed on to its progeny.

Environmental conditions also may have been a cause of the unusual irregularities found in the shortleaf x loblolly pine hybrids. Trees 1, 6-10 and 35 are the only ones located in California, and when ranked according to total irregularity all seven were among the nine most irregular trees studied. The genetic make-up of trees 21-23 (located in Texas) also includes material of slash pine along with that of shortleaf and loblolly pine. This should provide even greater conditions for irregularities to occur, but the total irregularity of these trees was quite low. It seems possible, therefore, that certain climatic conditions, such as temperature fluctuations, occur at the California location that adversely effect meiosis and thereby cause some of the irregularities observed in chromosome behavior.

Shortleaf pine was involved in the formation of 60 percent of the hybrids evaluated in this study. In comparing total irregularity, 70 percent of the 20 most irregular hybrids involved shortleaf pine, which suggests this species may be slightly less compatible than the others. Considerably more information must be obtained, however, before this can be verified.

Perhaps the most significant contribution of this study was the demonstration of a high level of tree to tree variation. For nearly every cross, this was of such a magnitude as to make comparisons between hybrid groups either difficult or impossible. The ranking of individuals within groups frequently differed by as many as 10 of the 30 places, and in some the differences were greater than 20. All but one of the hybrid groups contained at least two individuals that were either half- or full-sibs, and comparable differences were found even among such closely related trees. In the loblolly x slash pine hybrids, for example, trees 11-13 are full-sibs, and they differed in ranking by 13 places; the greatest difference in ranking for all trees of this combination was 21. Trees 16 and 17 (longleaf x slash pine hybrids) similarly are full-sibs, and they differed in ranking by 26 places.

The greatest manifestation of between tree variation occurred among trees 31-35 which were obtained from a three species cross of shortleaf, loblolly and slash pines. These hybrids all have a common seed parent, but the male parent is unknown because a pollen mix was used. The cross was made in California at the Institute of Forest Genetics, but the hybrids included in this section are located in two different areas; trees 31-34 are in the Fastrill Arboretum in Texas and tree 35 is in the Eddy Arboretum in California.

TABLE 1. Meiotic irregularity in species and hybrids (percent observed cells)

Tree Number	Species or Hybrid	Univalents	Lagging Chromosomes	Fragments	Bridges	Micronuclei	Total Irregularity	Irregularity Rank of Hybrids
1	P. echinata-V22	0	0.71	1.42	1.42	0	1.56	
2	P. palustris-4	1.16	0	0.20	0.26	0	0.39	
3	P. palustris-5	0.79	0	0	0.65	0	0.46	
4	P. taeda-C5	1.54	0.57	0.18	0.13	0.20	0.83	
5	P. taeda-84	0.39	0	0.20	0.26	0	0.52	
6	P. echinata x elliottii-10	1.40	6.49	0.84	1.05	12.19	8.30	3
7	P. echinata x taeda-5	5.10	0.39	3.54	1.18	1.20	4.30	5
8[a]	P. echinata x taeda-40	4.17	0.38	0.38	1.14	0.39	2.48	7
9[a]	P. echinata x taeda-60	1.90	2.95	0.37	2.35	2.11	3.76	6
10[a]	P. echinata x taeda-67	51.25	14.12	2.47	2.70	3.29	20.53	2
11[b]	P. taeda x P. elliottii-1	0.50	0	0.74	0	0.24	0.58	21
12[b]	P. taeda x P. elliottii-2	1.92	0.40	0.40	0.13	0.16	0.69	18
13[b]	P. taeda x P. elliottii-3	2.71	0.39	1.37	0.65	0.19	1.57	8
14	P. taeda x P. elliottii-4	0.78	0	0	0	0	0.19	29
15	P. taeda x P. elliottii-5	1.21	0	0	0	0.20	0.58	20
16[x]	P. palustris x P. elliottii-1	0	0	0.20	0	0	0.06	30
17[x]	P. palustris x P. elliottii-2	0.39	6.99	7.54	0.38	0.97	6.01	4
18[c]	P. (taeda x elliottii) x elliottii-1	2.44	0.66	0.22	0.98	0	1.48	10
19[c]	P. (taeda x elliottii) x elliottii-2	0	0.75	0	0.39	0.74	0.91	13
20[c]	P. (taeda x elliottii) x elliottii-3	0	0	0.78	0	0.20	0.33	24
21	P. (echinata x elliottii) x taeda-1	0.39	0.39	0.20	0.13	0.20	0.33	23
22[d]	P. (echinata x elliottii) x taeda-2	1.54	0.66	0.22	0.26	0.39	0.79	15
23[d]	P. (echinata x elliottii) x taeda-3	0	0	0.22	0.93	0.25	0.79	16
24[e]	P. echinata x sondereggeri-1	0.86	1.70	0.42	0.14	0.21	1.51	9
25[e]	P. echinata x sondereggeri-2	0.86	0	0.20	1.10	0.43	0.98	12
26	P. (palustris x elliottii) x wind-1	2.31	0	0	0.13	0	0.45	22
27	P. (palustris x elliottii) x wind-2	0.39	0.39	0	0.13	0	0.33	25
28[f]	P. (elliottii x echinata) x (echinata x elliottii)-1	0	0	1.23	0.33	0.74	0.83	14
29[f]	P. (elliottii x echinata) x (echinata x elliottii)-2	0.98	0	0.20	0.30	0.25	0.61	19
30[f]	P. (elliottii x echinata) x (echinata x elliottii)-3	0.39	0.20	0.39	0	0	0.33	26
31[z]	P. (echinata x taeda) x (echinata x elliottii)-1	0	0.25	0.74	0.65	0	0.76	17
32[z]	P. (echinata x taeda) x (echinata x elliottii)-2	1.48	1.47	0.49	0.49	0.25	1.23	11
33[z]	P. (echinata x elliottii) x (echinata x taeda)-3	0	0.20	0	0.33	0.25	0.33	27
34[z]	P. (echinata x taeda) x (echinata x elliottii)-4	0	0.20	0.25	0.17	0	0.25	28
35[z]	P. (echinata x taeda) x (echinata x elliottii)-5 (1962)	84.25	50.19	3.28	13.59	25.18	47.24	1
	" (1964)	88.75	37.99	10.07	14.95	32.41	60.38	
	" (1965)	83.94	58.31	6.65	6.32	21.72	53.80	

[a-f] Individuals with the same superscript are full-sibs

[x,z] Individuals with the same superscript are half-sibs

The magnitude of meiotic irregularity observed for tree 35 was the greatest ever reported for any pine. On the other hand, meiosis in trees 33 and 34 was no more irregular than normal species representatives. When ranked according to total meiotic irregularity, this group of half-sibs was so variable as to essentially cover the entire range observed in this and other comparable studies of pines. The irregularities, which for each stage were considerably greater in tree 35 than for any other tree, were studied for three different years. The results for each year were remarkably similar, which suggests that a genetic or chromosomal imbalance in this tree may be at least partly responsible for the occurrence of the anomalies. It should be noted, however, that the trees of this cross located in California are growing quite poorly in comparison to those in Texas. They are short, poorly formed, and their foliage is quite sparse. Such poor development indicates that a physiological incompatibility exists with the California environment, and this may be severe enough to also affect meiosis. It is difficult to say which factor is the most important; all quite likely are involved to some degree. A better evaluation of the situation will be possible when the remaining trees at Placerville become sexually mature.

The kinds of irregularities observed in tree 35 are illustrated in figures 1-9. As shown, all stages of the meiotic cycle were drastically disrupted. Univalents ranging in number from 1-24 occurred in more than 80 percent of the late diakinesis and metaphase I cells (Fig. 1 and 2). In fact, unpaired chromosomes occurred so frequently that it was difficult to find a normal metaphase figure in which all of the bivalents were properly aligned on the plate. Evidence of precocious disjunction was found at metaphase I, but in general, it appeared as if desynapsis occurred before the chromosomes reached the metaphase plate.

A very large proportion of the telophase I cells contained lagging chromosomes (Fig. 3 and 4) that very likely resulted from the irregularities that occurred during the earlier stages. Many of these chromosomes (Fig. 4) were single and must have resulted from early centromere division of the normally bipartite anaphase I chromosome.

Additional evidence of the disrupted movement of the chromosomes was found in the second division. In metaphase II chromosomes frequently were not oriented correctly on the equatorial plate (Fig. 6); in telophase II lagging chromosomes, nuclei of unequal sizes and chromatin bridges appeared (Fig. 7); micronuclei were quite abundant in both the dyad (Fig. 5) and the tetrad stages (Fig. 8); and small aborted and giant pollen grains (Fig. 9) occurred in frequencies greater than 20 percent.

Somewhat surprisingly, chromosome bridges were found to be very abundant in tree 35. Several factors might be responsible for this. If crossing over is partially localized as suggested by Saylor and Smith (1966), a breakdown of the control mechanism might allow more crossing over to occur with a subsequent increase in bridges if heterozygous paracentric inversions exist. Such a development could occur independently among progeny of a given cross. It is also possible that certain physiological processes have been altered in such a way as to make the chromosomes more susceptible to breakage and fusion which in turn produce chromosome bridges.

Variation in morphological traits that is independent of the degree of meiotic irregularity is demonstrated by comparing three of the shortleaf x loblolly hybrids. Trees 8-10 are 27 year old full-sibs that differ markedly in their appearance. Tree 9 is a bushy dwarf about two feet tall; tree 8 is a semi-dwarf approximately 15 feet tall that also is somewhat bushy in appearance; number 10 appears normal in all respects, and is about 60 feet tall. Although all three hybrids were among the seven most irregular trees in this study, there was considerable meiotic variation among them. Surprisingly, the morphologically aberrant trees were the most normal meiotically, while tree 10 was so irregular that it ranked as the second most irregular tree in the entire study. It is interesting to note that the common shortleaf parent (tree 1) has a past history of producing a high frequency of aberrant progeny. Because inversion bridges are noticeably frequent in this tree, it is tempting to speculate that the mutant types are the result of minute deficiencies or duplications in the chromosomes.

CONCLUSIONS

The results of this study indicate that loblolly, long-leaf, short-leaf and slash pines are compatible enough genetically and chromosomally to allow interspecific hybrids, including three-way crosses, to be formed and to develop normally. Although meiotic irregularities of some type were observed in every tree studied, they were in general only slightly more abundant in the hybrids than in the species representatives. Irregularities frequent enough to

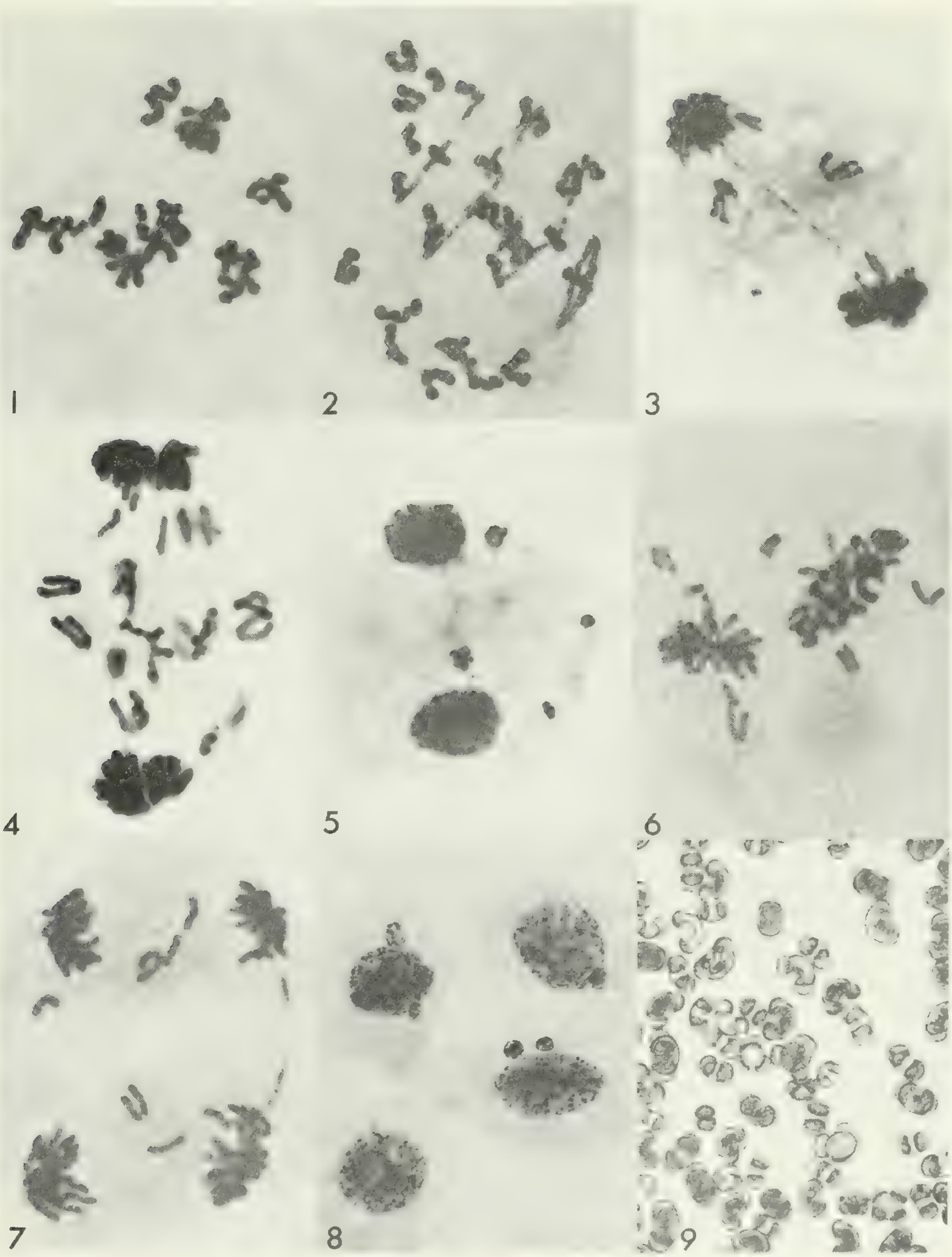

Fig. 1-9. Irregular meiotic divisions in P. (echinata x taeda) x (echinata x elliottii)--tree 35.

1. Diakinesis: unpaired chromosomes, X 625.
2. Metaphase I: univalents and nonsynchronous separation of chromosomes of different bivalents, X 625.
3. Telophase I: lagging chromosomes, and inversion bridge with accompanying acentric fragment, X 575.
4. Telophase I: lagging chromosomes, and precocious centromere division, X 625.
5. Dyad: micronuclei, and chromatin bridge, X 575.
6. Metaphase II: lagging chromosomes, X 625.
7. Telophase II: lagging chromosomes, and inversion bridge persisting from the first division, X 625.
8. Tetrad: micronuclei, X 495.
9. Pollen: normal, giant and aborted pollen grains, X 67.

adversely affect gamete formation to any degree were found in only one tree, and this was a three species hybrid that had at least two half-sib relatives that were quite normal. Although somewhat of an extreme case, this exemplifies the high level of tree to tree variation found in all such studies made by this investigator. These results are also in agreement with studies of between tree variation in other characteristics.

It would appear, therefore, that genetically or chromosomally induced meiotic abberations that lead to inviable gametes are not a major barrier to the exchange of genetic material among these southern pines. The need for care in selecting parents, especially for advance crosses, is demonstrated, however, by the range of variation found among closely related individuals of a given type.

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Initial Results of Slash Pine Progeny Tests Replicated in Time and Space

RAY E. GODDARD and FRANK VANDE LINDE[1]

Progeny tests are essential features of the southern pine improvement programs currently in progress. Most of the parent trees used in the programs were selected in wild stands. As discussed in detail by Squillace[2] these selections were made on phenotypic appearance with little knowledge of the breeding value of trees chosen. Such information as was available on genetic variances was obtained from planted tests under environmental conditions having little similarity to those in natural stands. Selections were made on the basis of educated guesses as to their desirability for inclusion in an orchard. Final decisions concerning the validity of each selection must rest upon the value of progenies produced.

The objective of progeny testing is quite simple. Tests should be designed to show the breeding value of the various selections used in an orchard program. That is, tests should demonstrate the extent that the desirable characteristics of the parent trees are passed on to their offspring. With the arrangement of clones in our current orchards, genetic improvement depends on additive genetic variance and the ability of selections to combine well with numerous other selections. Clones are scattered more or less randomly over an orchard; thus, the crossing of any two specific clones which combine to produce exceptionally fine offspring can be expected to occur only occasionally and can have but little impact on the mean performance of orchard progeny. On the other hand, use of clones in an orchard that produce outstanding progenies almost regardless of pollen parent will mean substantial improvement in genetic quality. Progeny tests will supply information needed to rogue orchards or establish new ones without the guesswork unavoidable when current programs were initiated.

For very accurate determination of breeding values, too many progenies can hardly be established and observed. However, progeny testing is expensive and involves much meticulous work and careful observation. From a practical standpoint, testing beyond the point of reasonably accurate estimates of the breeding value of the various selected parents cannot be justified. As results come in from early tests, they will establish a basis for compromise between the requirement for accurate evaluation and the expense of testing.

DESCRIPTION OF TESTS

To aid cooperators in the University of Florida forest tree improvement program, progeny testing guidelines were drawn several years ago. As is so often the case, no fully proven procedures were established and methods were needed which appeared to fit the existing circumstances. Orchards were beginning to produce cones but some trees produced cones sooner and in much greater quantity than others. Also, most cooperators had 75 or more selected clones and simultaneous testing of such large numbers of lines would be quite unwieldy, even if progenies were available from all of them. Delay until all clones became productive was not warranted; for progeny tests would not be started yet if we had waited. Thus, a testing plan was needed to utilize seed as it became available and avoid excessive testing of the early and highly productive clones.

The plan provided for the inclusion of progeny of each clone in a minimum of three tests. Tests were to be established on contrasting sites and during more than one establishment year. The plan suggested, for example, the initiation of two tests in one year on different sites and planting a third test a year or more later. No two tests needed, necessarily, to include exactly the same set of clonal progenies.

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[2] 9th Southern Conference on Forest Tree Improvement.

Provision was made for use of any one of three types of progenies – open-pollination in the seed orchard, poly-mix, or controlled crosses using tester pollens. For open-pollinated and poly-mix progenies, ten randomized blocks of 10-tree row-plots were suggested. Following this procedure, 100 seedlings of a clone would be established per test, and a minimum of 300 seedlings in combined tests for the evaluation of a clone.

The Florida progeny testing plan proposed the repetition of at least two check sources in each test. Seed for one check lot, used by all cooperators in the Florida program, was from a seed production area in Long County, Georgia, established by Continental Can Company. In addition, it was suggested that each cooperator draw sufficient seed from their current nursery supply for repeated use as a second check lot. Each check lot was established in at least two plots in each block of each test.

Tentatively scheduled were measurements at one, three, five, ten and fifteen years of age. Most tests were recently established and only a few are over two years old. Among the older tests are those established by Brunswick Pulp and Paper Company.

The progeny testing plan adopted by the Brunswick Pulp and Paper Company was reasonably close to the suggested outline. Open-pollinated progenies of individual clones in the company slash pine orchard were used for test establishment. In 1963, two sites were planted with ten blocks at each site. In 1964 and subsequent years, two sites were planted with only five blocks per site with the provision that test establishment would be continued until progeny of each clone had been planted three years. Thus, each progeny lot would appear in two 5-block tests per year for three years – 6 tests for each lot. This variation of the general plan provided a broader sampling of sites than the original proposal but established essentially the same number of seedlings for the evaluation of individual clones.

In addition to the uniform check lot used by all cooperators and the check lot drawn from seed used in the company nursery, since 1964 a third check lot, seed from a company seed production area, were included in all tests.

Data on certain progenies in Brunswick Pulp and Paper Company Tests 3, 4, 6, 7, 8, 9, 10, 11, established 1963 through 1966, are discussed in this paper. The discussion is limited to growth as indicated by total seedling height one and three years after field planting. Although a number of progeny lots were included in each of the several tests, only six were common to all four tests established in 1963 and 1964 for which third year measurements were available. In the six tests established 1964 through 1966, there were 24 lots common to all tests. For these lots data were available on height after one growing season in the field.

All tests were established on previously wooded sites. The normal site preparation procedures of Brunswick Pulp and Paper Company were followed. After the stands were harvested, remaining trees were removed with K-G blades and the sites were raked, harrowed, and bedded.

The sites were typical of the lower coastal plains in southeastern Georgia. Soil site estimates, soil profile description, and drainage classes at each test site are presented in table 1.

TABLE 1. DESCRIPTION OF TEST SITES

Test	Year Planted	Soil site index at age 25	Drainage Class	Soil Description
3	1963	60	Well drained	Sand over sandy clay at 4 to 5 feet
4	1963	65	Moderately well drained	Sand over sandy clay at 2½ to 3 feet
6	1964	65	Well drained	Loamy sand over sandy loam at 4 to 5 feet
7	1964	60	Moderately well drained	Sand over loamy sand with cemented hardpan at 18 inches
8	1965	70	Imperfectly drained	Loamy sand over sandy clay at 5 to 6 feet
9	1965	70	Imperfectly drained	Sand over loamy sand with 2 uncemented hardpans-one at 12 inches and one at 5 feet
10	1966	65	Imperfectly drained	Sand over loamy sand with uncemented pan at 18 inches
11	1966	65	Moderately well drained	Loamy sand over sandy clay at 4 feet

DATA ANALYSIS

Analytical procedures planned for these and other tests were analysis of variance coupled with a multiple range test to distinquish progenies performing significantly better than check lots. Each test is a complete experiment and will stand alone. Also, lots common to two or more tests can be included in combined analyses. A combined analysis is illustrated in (Table 2) concerned with first year heights of 24 lots which were established in six separate tests.

In combined tests with common progeny lots, it is possible to partition the environmental variance. This is not a major objective of progeny testing, for the purpose is testing lots, not planting sites. However, by looking at environmental variation, improved testing procedures may be indicated.

Very pertinent to progeny testing is the interaction between progeny lots and the various environmental conditions. Preferable at the present stage of development would be lots which are superior in all test environments rather than those which respond well under some conditions but not under others. Effective progeny testing must point out such possible interactions.

Of special note is the error term used in testing for significant differences in the analysis of variance and in multiple range tests. At least two plots of each check lot were included in each block of every test. Additional check plots were included in several tests to square off the blocks. These check lots serve as a common yardstick for the evaluation of clonal progenies only if they have sufficiently broad genetic adaptation not to interact widely with the various environmental conditions. Plots of a check within a block will vary due to within block differences, lack of genetic identity of seedlings in the several plots and other chance circumstances. If the check plots validly indicate random variables, the variance of check lots provides the best estimate of experimental error for general conclusions. The block-lot interactions, commonly used as an error term, supply inferences more specific to the test site, and the variance of trees within plots is cumbersome and probably overly sensitive. As employed in these tests, check plots serve the dual purpose of estimating experimental error and of providing a basis for determination of the relative desirability of select lots.

TABLE 2. ANALYSIS OF VARIANCE OF FIRST YEAR HEIGHTS

	Degrees of Freedom	Sum of Squares	Mean Square
Progeny lots	23	3.0762	0.1337**
Environments	5	66.0564	13.2112**
Sites planted 1964	1	11.2200	11.2200**
Sites planted 1965	1	13.2605	13.2605**
Sites planted 1966	1	8.4429	8.4429**
Years and Sites	2	33.1331	16.5665**
Interaction (L x E)	115	9.2686	0.0805**
L x 1964 sites	23	0.8585	0.0373
L x 1965 sites	23	3.5325	0.1535**
L x 1966 sites	23	0.3753	0.0163
L x sites and years	46	4.5023	0.0978**
Variance of checks (error)	310	9.2702	0.0299

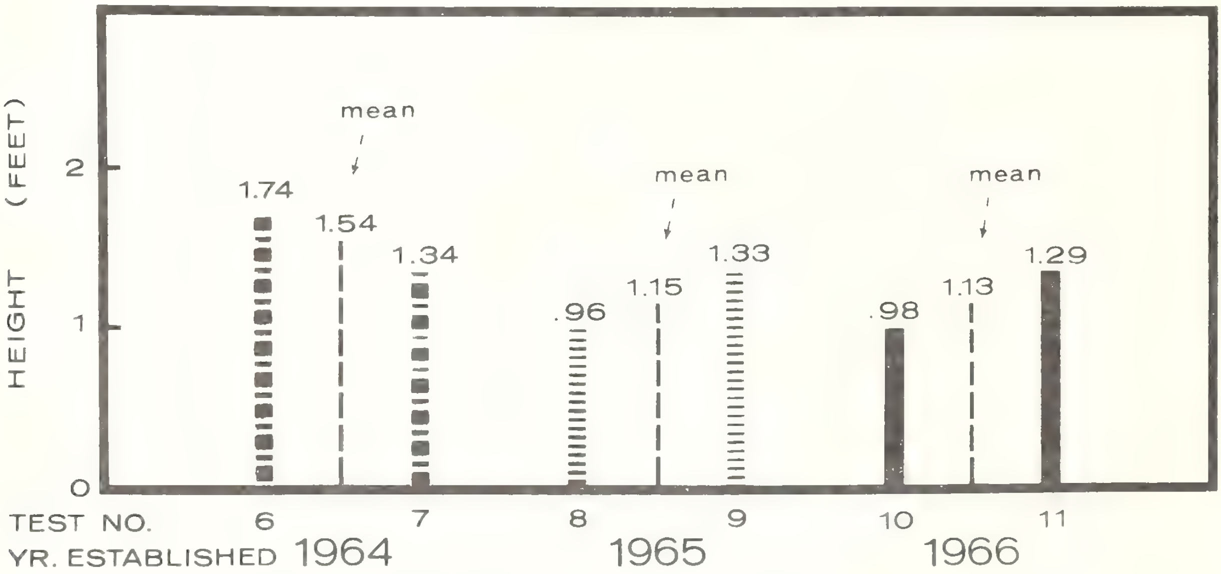
** Significant at the 1% level.

RESULTS AND CONCLUSIONS

As only the Brunswick Pulp and Paper Company is directly concerned with the individual lot differences in these tests, it is sufficient to indicate that significant differences among lots were apparent in both one year and three year heights. Progenies of about one-half of the select trees were rather consistently superior in height to the average of the check lots.

The ranges in mean height were not large – 0.20 feet at one year and 0.66 feet at three years. The differences have little economic significance except as indices of possible future behavior.

Mean height at one year of 24 progeny lots established in 6 tests.



The height growth indicated that the total environments tested were quite different (see Figure 1). The best first year growth was obtained in test 6 and first year growth was greater on both sites planted in 1964 than it was on sites planted in 1965 and 1966. In these tests, the effects of site and of year of establishment are confounded. It is impossible to tell whether the better growth in 1964 should be attributed to superior weather conditions that year or, possibly, to the better growth conditions on the sites on which the tests were established. Probably, it was the combined effect of both factors. Similarly, differences noted in average growth between tests established the same year may be, in part, influenced by variation in local weather conditions. It may be noted that neither first nor third year heights were related to the several site evaluation factors except, possibly, drainage class. It is of possible significance that approximately half of the sum of squares for environments (Table 2) was contributed by the combined effects of sites and year of establishment, suggesting a possible strong influence of establishment season on first year growth.

Third year data were much more limited with only six lots involved. Height growth was not significantly different on sites planted in 1963 (Table 3). Growth was significantly different on sites planted in 1964 and the combined effect of establishment year and site was very highly significant. It must be remembered that trees in these tests were growing in 1964 and 1965. Therefore, the two sites planted in 1964 were inferior to those planted in 1963 for seedling growth (see Table 4), the effects of weather conditions during the establishment year carried over into subsequent years, or local weather conditions at the individual test sites were strongly affecting growth. Again, the apparent results were probably influenced by a combination of factors.

The manner in which the various progeny lots reacted to these environmental differences is of particular interest and special importance. These reactions or lack of reactions will have a deciding influence on the make-up of second or third generation seed orchards. In tests 6 through 11, the interaction of 24 lots with 6 environments in first year height was highly significant (Table 2). The largest portion of the interaction sum of squares was contributed by the confounded effect of sites and establishment years. Figures 2-4 illustrate the interactions observed. Note particularly the shifts in relative heights of lots between the two 1965 tests.

TABLE 3. ANALYSIS OF VARIANCE OF THIRD YEAR HEIGHTS

	Degrees of Freedom	Sum of Squares	Mean Square
Progeny Lots	5	11.1609	2.2321**
Environments	3	226.9241	75.6413**
Sites planted 1963	1	1.1628	1.1628
Sites planted 1964	1	19.4168	19.4168**
Years and sites	1	206.3445	206.3445**
Interaction (L x E)	15	1.6161	0.1077
Blocks	26	100.3524	3.8597
Lots X Blocks	130	50.9300	0.3917
Variance of checks (Error)	78	31.9682	0.4098

In contrast to the vagaries of relative ranking of height growth after one year, the interaction of the six lots for which third year height data were available with sites was not significant. As indicated in Table 4, lots 4 and 5 had the greatest height and lot 12 had the least height at each location. Approximately the same conclusions could be drawn concerning the relative value of the lots involved from each individual test as from the combined analysis.

These data are insufficient for firm recommendations, but, if established tests continue to show a decline in the interaction between lot and environment with increasing age, some changes in test procedures may be warranted. First year data are of little significance except for possible differences in rates of survival and of disease. Unless first year height measurements predict future growth potential, the expense of recording and analysis of data at this stage is not justified.

The sites on which these tests were established were by no means identical. Yet they represent a relatively narrow range of site qualities (60 to 70 at age 25). The admittedly shaky evidence presented here suggests that environmental differences were too small to differentially affect growth of the various progenies after one year. Repeated testing, even in different years, on similar sites would appear to increase the accuracy of evaluation of parental clones only slightly. Assuming that other tests will substantiate this conclusion, no more than two well designed tests established on

TABLE 4. MEAN HEIGHT IN FEET AND RELATIVE RANKING OF 6 PROGENY LOTS AFTER 3 YEARS IN 4 TESTS.

Progeny Lot	Test 3		Test 4		Test 6		Test 7		Combined Tests	
	Mean	Rank	Mean	Rank	Mean	Rank	Mean	Rank	Mean	Rank
4	6.70	2	6.78	1	5.37	1	4.26	2	5.78	2
5	6.77	1	6.60	2	5.31	2	4.53	1	5.80	1
6	6.46	4	6.33	4	4.59	5	4.06	4	5.36	5
12	6.35	6	5.87	6	4.50	6	3.86	6	5.14	6
13	6.58	3	6.24	5	5.41	3	4.22	3	5.61	3
14	6.38	5	6.39	3	5.05	4	4.16	5	5.50	4
Mean	6.53		6.36		5.08		4.13			

One-year heights of two progeny lots
Expressed as percentage of mean check height

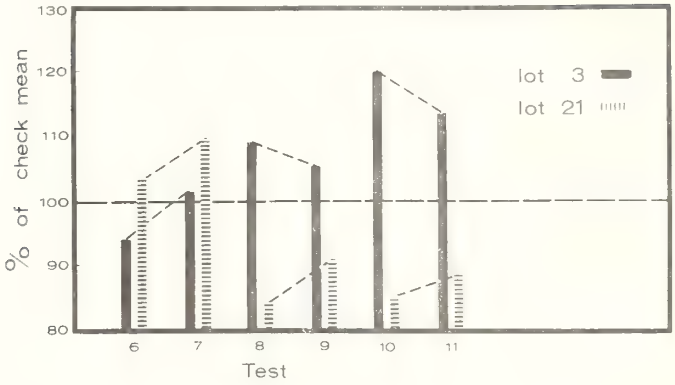


FIGURE 2

One-year heights of two progeny lots
Expressed as percentage of mean check height

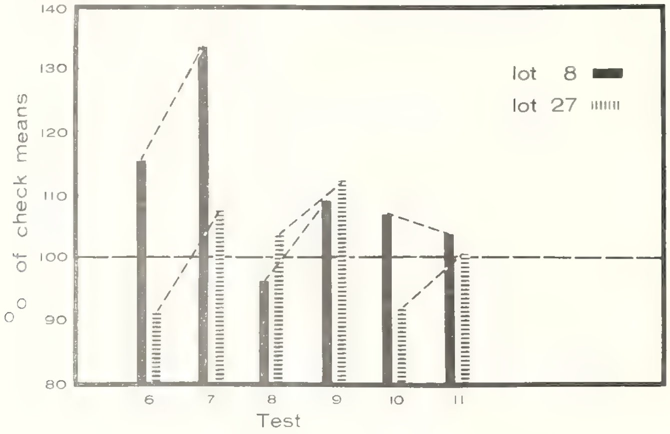


FIGURE 3

One-year heights of two progeny lots
Expressed as percentage of mean check height

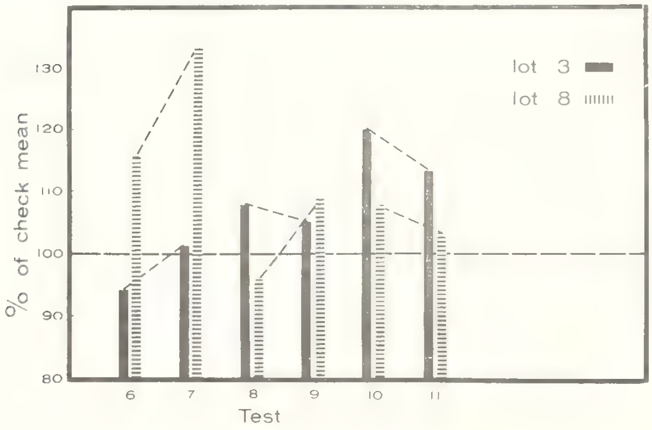


FIGURE 4

sites typical of those of most common occurrence in an area should be sufficient to evaluate the improvement potential of seed orchard clones for planting average sites. For indications of variaation in adaptibility to environmental conditions, it will probably be necessary to establish tests over a greater geographic range on sites of more diversity than those employed in these tests.

SUMMARY

Height measurements one and three years after establishment were analyzed for eight slash pine progeny tests established on different sites from 1963 to 1966.

Growth at both ages was significantly different on the various test sites. One year after establishment, the interaction of progeny lots and environments was highly significant. Results suggest a variable response to seasonal weather conditions and to site factors in early growth.

The progeny lot and environment interaction was not significant for height at three years. Possibly, more diverse sites should be tested to determine variation in response.

The Application of Tissue Culture Techniques to Various Problems in Forest Tree Improvement

CLAUD L. BROWN[1]

Tissue culture techniques have become a valuable tool in studies of plant growth and development. Today, with our knowledge of plant nutrition it is possible to culture cells, tissues and organs of many plants for indefinite periods of time. The cells and tissues of some species are easily grown on a relatively simple synthetic medium, whereas those from other species may require combinations of complex growth factors, and still the tissues of other species are cultured with much difficulty or not at all.

To the physiologist and developmental morphologist, tissue culture techniques have been extremely useful in studying certain aspects of plant nutrition, the biogenesis of numerous cellular components, and various processes involved in tissue and organ differentiation. To the geneticist and cytologist, **in vitro** cultures have been useful from time to time to nurse excised hybrid embryos to maturity which would otherwise have aborted because of their incompatibility with maternal tissues. In addition, cell and tissue cultures have proved of much utility in studies of chromosome morphology, ploidy, somatic mutations, and tumor formation.

I wish to limit this discussion on the use of sterile culture techniques to two major problems directly related to the progress of tree improvement: 1) the vegetative propagation of clonal material, and 2) the production of homozygous diploids.

Propagation of Clonal Material

One of the most time consuming and costly procedures used in the establishment of clonal orchards is the process of grafting. The many problems associated with graft success and failure are well-known to tree improvement foresters. Fortunately some woody species can be propagated with ease from stem cuttings or juvenile stump sprouts. For these species clonal multiplication is no problem. But in other species, expecially many of the pines, rootability is so low that clonal lines can only be established through grafting.

Real progress is now being made in propagating difficult to root species, includina conifers, through the use of tissue culture techniques, but the real breakthrough has not yet arrived. For example, in our laboratory we have spent considerable time during the past four years developing a synthetic medium for the rapid continuous growth of longleaf, slash, and loblolly pine callus. Only during the past year has a defined medium been developed that supports excellent growth of these species (Table 1). Since this was achieved, we have been able to culture successfully members of 15 genera of gymnosperms out of the 21 genera tested from various parts of the world.[2]

The reason we are so enthusiastic about the establishment of rapidly growing callus cultures of pine tissues lies in the fact that those of us engaged in this type of work have often observed a high correlation between species "rootability" and ease of establishing tissue cultures. Stated differently, given a species that roots easily, e. g. willow, aspen, red maple, etc. it is likely that its cells will also culture with ease. Conversely, those species that root with difficulty, usually culture poorly or not at all. Such was the case with the southern pines, but now that we know more about their cultural requirements **in vitro** it is probable that we will soon be able to induce bud and root formation in callus cultures.

The classical work of Skoog and Miller (1957) showing the effects of a proper balance of indole-3-acetic acid (IAA) and cytokinin (kinetin) on root and bud formation in tobacco callus can now be used with modifications to produce similar effects in certain hardwood cultures (cottonwood and red maple), but so far we have not yet worked out the proper conditions to induce either bud or root formation in the callus cultures of pine. This is not too discouraging, however, because we know that achieving the precise balance of growth factors for producing pine plantlets is no simple undertaking. It is only a matter of time before such can be accomplished.

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[2] Unpublished results of C. L. Brown and J. Mustoe, University of Georgia.

Table 1. Composition of medium used for culturing longleaf pine callus. Modified from Murashige and Skoog (1962).

Inorganic Nutrients	mg/liter	Organic Supplements	mg/liter
NH_4NO_3	1650		
		Nicotinic acid	0.5
KNO_3	1900	Pyridoxin-HCl	0.1
		Thiamin-HCl	0.1
$CaCl_2.2H_2O$	440		
$MgSO_4.7H_2O$	370		
		Kinetin	.5
KH_2PO_4	170	2,4-D	5.0
		Inositol	100.0
		Asparagine	100.0
		Sucrose (2%)	20000
H_3BO_3	6.2	Agar (0.8%)	8000
$MnSO_4.4H_2O$	22.3		
		(pH 5.7-5.8)	
$ZnSO_4.4H_2O$	8.6		
KI	0.83		
$Na_2MnO_4.2H_2O$	0.25		
$CuSO_4.5H_2O$	0.025		
$CoCl_2.6H_2O$	0.025		
$FeSO_4.7H_2O$	27.8*		
Na_2-EDTA	37.3*		

* 5 ml of a stock solution containing 5.57 g $FeSO_4.7H_2O$ and 7.45 g Na_2-EDTA per liter of H_2O.

In attempts to carry this work further, i. e. , the mass production of diploid plantlets in laboratory flasks, we have used the approach of Steward and his colleagues (Steward et al, 1958) where they were successful in growing whole carrot plants from small aggregates of cells, or even from single cells, in liquid suspension cultures. Although we have only recently (within the past 3 months) been able to establish liquid suspension cultures of longleaf pine, we can now grow hundreds of thousands of small cell colonies all with the same genotype in a few small flasks under controlled laboratory conditions. It seems only a matter of time before one will be able to propagate, by the thousands, many of the difficult to root species with considerable facility and little expense. This possibility is real, and these techniques will undoubtedly be used more and more in forest genetics, agronomy, and horticulture. The production of a few thousand plantlets from a single mass of cultured body cells from superior pines, or from hybrid orchids would be equally exciting and economically rewarding to foresters and horticulturists.

Culture of Haploid Tissues and the Development of Homozygous Diploid Lines

In addition to mass propagating selected heterozygous clones, it is now possible to grow haploid tissues (callus cultures) of higher plants. It is significant and encouraging that the gametophyte cells of a woody plant species and especially a gymnosperm (Ginkgo), was the first to be cultured on artificial media. Tulecke (1957) successfully established pollen cultures of Ginkgo on a fairly complex medium, and more recently, he has been able to grow the female gametophyte of the same species under similar conditions (Tulecke, 1964). So far in our laboratory we have been unable to establish pollen cultures of any native pine on media similar to that used by Tulecke for Ginkgo. Neither have we been able to establish pollen cultures from any woody or herbaceous angiosperm although we have attempted to grow numerous species from a wide array of plant families beginning with members of the primitive **Magnoliaceae** through the highly advanced **Scrophulriaceae.** There is still hope, however, because over three years ago one of my students was able to obtain excellent proliferation of the female gametophyte of longleaf pine under certain conditions. Since that time we have been able to keep this haploid tissue growing fairly well for about 5 transfers (six months) before finally losing it.

Thus, we have not given up on the possibility of growing haploid tissues of pines and hardwoods because of the extremely important application of these procedures to forest genetics. With the production of haploid tissues, followed by chromosome doubling, and the formation of plantlets (roots and buds), a homozygous line would be effectively produced. This alone would by-pass a century or more of inbreeding in forest trees, and in the case of exceptionally desirable superior hybrids permit the forest geneticist to establish a true-breeding line almost overnight. Although I am well aware of the pitfalls in the widespread use of the monocultures, and the fact that some of our fellow foresters might be quite perturbed over the commercial use of homozygous lines, many of us working in tree physiology and genetics would be more than elated to have such material available for experimental purposes. Although it is hazardous for the researcher to make predictions or attempt to out-guess the plants with which he works, I would like to emphasize the fact that the scientific know-how for producing haploid tissues, and the control of plantlet formation is real. Logically it is only a matter of time (probably 3-5 years) before the production of homozygous lines in forest trees, horticultural plants, or agronomic crops becomes a reality through the use of tissue culture techniques.

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Cone and Seed Yields from F_1 Crosses Involving Five and Six Year Old Open and Controlled-Pollinated Seedlings of Loblolly Pines

JAMES T. GREENE[1/]

In the establishment of breeding programs, distinct from vegetative propagation, it is apparent that any means which will shorten the time of progeny to a stage of flowering and to the increase of amount of seed production will be of great importance. Most loblolly pine (**Pinus taeda L.**) trees begin to produce strobili at an age of about 8 to 10 years.

Righter (1939) reported the average of the minimum ages of ovulate flower production for 55 species and varieties of pine to be 5.2 years. The earliest reported ages of flower production in loblolly pine were 5 years for ovulate flowers and 6 years for staminate flowers.

Mergen (1961) reported on the stimulation of early flowering in 3-year-old slash (**Pinus elliottii** Engelm.) and loblolly pines in a greenhouse, by keeping them under a high level of nitrogen nutrition. In commenting on these observations, Mergen concluded that, "(1) the ability to flower at an early age is genetically controlled, and (2) in flowering trees, the mechanism that controls the change from a vegetative shoot to a sexual one can be modified to some extent by the environment."

To determine if and how a particular characteristic is inherited, the forest geneticist must select and breed for a particular characteristic. The ultimate goal will be to incorporate desired characteristics, whatever they may be, into a particular genetic strain. By selection and controlled pollination, it should be possible to reduce "flowering" age considerably. This will save valuable years in tree improvement program as well as insuring early seed production in a grafted or a controlled-pollinated seedling seed orchard.

Greene and Porterfield (1962) located loblolly pines ranging from 21 to 30 years of age on the property of the University of Georgia which yielded seed that produced "seedlings" bearing female strobili at ages of three and four years from seed. One three-year-old loblolly pine seedling produced female strobili in 1959, after two years in the field. These strobili were crossed back to one of the early cone-producing parents. Two cones from this cross were collected in late 1960. The cones yielded 102 seeds. These seeds produced 44 normal seedlings. After five years in the field, 40 of these seedlings are growing and appear exceedingly vigorous. Approximately 75 per cent of these five-year-old seedlings are producing male and female strobili. This same seedling parent has produced female strobili for seven consecutive years.

Greene (1966) reported on the seed yield and plantable seedlings from controlled and open-pollinated four and five-year-old seedlings of loblolly and shortleaf (**Pinus echinata** Mill.) pines. These young "parents" were three and four years from seed when the pollinations were made.

Greene further reported that seventy-seven per cent of the controlled pollinations made in 1963 on four-year-old loblolly pines were successful. These crosses were F_2 and backcrosses.

Progenies from controlled crosses now growing on the property of the University of Georgia offer excellent opportunities to select for desired characteristics. Approximately 140 possible combinations are now growing in the field resulting from control-pollinations of loblolly, shortleaf, slash, and longleaf pine (**Pinus palustris** Mill.) trees.

RESULTS AND DISCUSSION

The following data illustrate that controlled-pollinations and seed set can be successfully accomplished on five- and six-year-old loblolly pine "seedlings." These data further indicate that "flowering" age of loblolly pines can be reduced through selection and controlled-pollinations.

The first part of the paper consists of information relative to type of cross, open- and controlled-pollinated cones and seed yields from five-year-old "parents." The progenies had been outplanted for

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five years when the cones were collected. This indicates the progenies were producing male and female strobili at four years from seed.

Cone and seed yields from the controlled- and open-pollinated crosses involving the five-year-old loblolly pines are summarized in Table 1. Sixty-five per cent of the controlled-pollinations made on these young F_1 parents were successful. These

Table 1. Controlled and Open-Pollinated Loblolly Pine Cones Collected in 1965 from 5-Year-Old Open- and Controlled Pollinated Seedlings.

Female	Male	Seed Parents	Type of Cross	Cones	Seeds Per Seedling	Seeds Per Cone
				NUMBER		
L-72XL-77	L-72	6	Backcross	14	43	18
L-72XL-77	Wind	2	Open	2	32	32
L-72XWind	L-72	13	Backcross	55	77	18
L-72XWind	Wind	4	Open	7	105	60
L-72XL-78	L-72	11	Backcross	15	18	13
L-72XL-78	Wind	2	Open	4	56	56
L-72XL-64	L-72	6	Backcross	17	51	18
L-77XL-72	L-77	11	Backcross	20	40	22
L-77XL-79	L-77	8	Backcross	26	40	12
L-77XL-79	Wind	1	Open	2	86	43
L-77XWind	L-77	9	Backcross	20	32	14
L-77XL-78	Wind	1	Open	1	137	137
L-77XL-78	L-77	1	Backcross	6	24	4
L-65XL-78	L-65	7	Backcross	22	68	22
L-65XL-78	Wind	2	Open	2	64	64
L-65XL-78	L-64XL-78	1	F_2	12	552	46
L-65XL-65	L-65	4	Backcross	19	73	15
L-65XL-64	L-65	2	Backcross	3	57	38
L-65XL-64	Wind	5	Open	13	149	57
L-65XWind	Wind	2	Open	5	159	64
L-65XWind	L-65	5	Backcross	12	24	12
L-79XL-79	L-79	4	Backcross	13	14	4
L-79XWind	Wind	8	Open	28	220	63
L-79XWind	L-79	2	Backcross	21	22	2
L-69XL-72	Wind	8	Open	34	300	71
L-69XL-72	L-72	14	Backcross	62	32	7
L-69XL-72	L-72XWind	2	F_2	9	510	113
L-69XWind	Wind	4	Open	11	197	72
L-69XL-72	L-69	4	Backcross	17	124	29
L-69XL-77	Wind	7	Open	19	161	59
L-69XL-77	L-77	4	Backcross	8	33	16
L-69XL-77	L-69	2	Backcross	7	19	5
L-64XL-78	Wind	3	Open	4	74	55
L-64XL-78	L-64	5	Backcross	12	35	15
L-64XL-78	L-64XL-78	2	F_2	18	540	60

Table 2. Controlled-and Open-Pollinated Loblolly Pine Cones Collected from 6-Year-Old Open-and Controlled-Pollinated Seedlings.

Female	Male	Seed Parents	Type of Cross	Cones	Seeds Per Seedling	Seeds Per Cone
				NUMBER		
L-69xL-77	L-77xL-79	5	F_2	10	125	63
L-69xL-77	L-69xWind	3	F_2	8	175	66
L-69xWind	Wind	5	Open	21	353	84
L-69xL-77	L-77	1	Backcross	1	11	11
L-69xL-65	L-65	1	Backcross	1	12	12
L-69xL-65	L-69	2	Backcross	2	3	3
L-69xL-64	L-69xWind	1	F_2	2	183	92
L-69xL-72	L-69xWind	3	F_2	11	250	68
L-69xL-72	L-72xWind	7	F_2	27	207	54
L-69xL-72	Wind	8	Open	27	236	70
L-69xL-72	L-69	6	Backcross	16	10	4
L-72xWind	L-77xL-79	4	F_2	4	153	77
L-72xL-78	L-78	3	Backcross	6	13	7
L-79xWind	Wind	4	Open	10	249	100
L-79xL-79	Wind	3	Open	16	422	79
L-79xL-79	L-79	17	Backcross	73	147	34
L-79xWind	L-79	18	Backcross	71	108	27
L-79xL-72	L-77xL-79	2	F_2	9	69	15
L-79xL-77	L-77xL-79	4	F_2	8	56	28
L-77xWind	Wind	1	Open	4	327	82
L-77xL-72	L-77xL-79	2	F_2	5	130	52
L-77xL-78	LongleafxLoblolly	2	F_2 - interspecific	2	38	38
L-77xL-78	L-77xL-79	7	F_2	7	169	72
L-77xL-78	L-78	8	Backcross	13	15	9
L-77xL-78	L-77	2	Backcross	11	48	9
L-77xL-78	L-78xWind	4	F_2	7	101	58
L-77xL-78	L-78xL-77	2	F_2	9	239	53
L-77xL-79	Wind	3	Open	14	352	76
L-77xL-79	L-77xL-79	4	F_2	8	114	57
L-77xL-79	L-79	14	Backcross	29	58	28
L-77xL-79	L-77	8	Backcross	8	26	13
L-78xL-77	L-78xL-77	4	F_2	5	57	45
L-69xWind	LongleafxLoblolly	7	F_2- interspecific	22	144	46
LongleafxLoblolly	LongleafxLoblolly	3	F_2- interspecific	23	261	34
LoblollyxSlash	LongleafxLoblolly	4	F_2-interspecific	8	88	44

crosses were F_2 and backcrosses.

Backcrossing is the crossing of a hybrid to one of its parental types. The F_2 is obtained by crossing among or selfing the F_1 individuals.

The number of open-pollinated seeds per individual "seedling" ranged from 32 to 300. The range in seeds per cone per individual parent was from 32 to 137. The range in seeds for individual F_2 crosses was from 510 to 552. The range in seeds per cone per individual F_2 cross was from 46 to 113. Backcrossing for individual parents resulted in a range of of seeds numbering from 14 to 124. The range in seeds per cone per individual backcross was from 2 to 38.

The second part of the paper consists of information relative to controlled- and open-pollinated cones and seed yields involving six-year-old parents. Approximately seventy per cent of the controlled-pollinations involving the six-year-old parents were successful. The progenies had been outplanted for six years when the cones were collected, which means the pollinations were made when the seedlings had been outplanted for five years.

Cone and seed yields from the controlled- and open-pollinated crosses involving the six-year-old loblolly pine seedlings are summarized in table 2.

The range in open-pollinated seeds per individual was from 236 to 422. Range in seeds per cone per individual was from 61 to 100. The range in seeds for individual F_2 crosses was from 56 to 250. The range in seeds per cone per individual F_2 cross was from 15 to 91. Backcrossing for individual parents resulted in a range of seeds numbering from 2 to 147.

Some interspecies pollinations were included in Table 2 to illustrate that viable seeds can be obtained through these F_2 multiple-species crosses. For example, (loblolly x slash) X (longleaf x loblolly) yielded 44 seeds per cone. (Longleaf x loblolly) X (longleaf x loblolly) yielded 34 seeds per cone. These parents were five-years-old when the pollinations were made. These interspecies crosses indicate the possibility of commercial potentialities in the South.

SUMMARY

These date illustrate that controlled-pollinations and seed set can be successfully accomplished on five- and six-year-old loblolly pine "seedlings." These data further indicate that "flowering" age can be reduced and fecundity rate can be improved through selection and controlled-pollinations for these desirable traits. These data prove that it is possible to produce F_2 seed in five or six years. We now have growing in the field 31 loblolly pine progeny groups from three and four-year-old parents.

An opportunity for reducing age of "flowering" and increasing fecundity rates in loblolly pines exists in the selection, control-pollination and progeny testing for these traits. This possibility has great utility in programs of tree improvement and especially from the practical aspect of producing commercial quantities of improved seed from "seedling" orchards. As someone has so aptly written, "our limitations are the limitations of our scientific insight and imagination, rather than of the biological material with which we work."

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Wood Density and Percent Summerwood Variation Among Nine Loblolly Pine Seed Sources Grown in Alabama

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Since the establishment of the Southwide Pine Seed Source Study in 1951, information concerning racial difference in external characteristics of the major southern pines has become increasingly available. Equally important to woodland managers is information on the intrinsic qualities of the wood in the juvenile and mature parts of the trees. Such information can also be obtained from the Southwide Pine Seed Source Study now that most of the plantings have reached an age at which wood properties of the juvenile zone of the tree can be evaluated reliably. Numerous reports indicate that wood properties and anatomical characteristics vary over broad geographic areas (3, 4, 7, 13, 14, 15). This variation has been attributed to climatic and physiographic differences. Until now, few data have been obtained on the influence of racial factors on the intrinsic qualities of wood because of the limited availability of seed source study material. This paper presents data on wood density and percent summerwood variation from one central Alabama planting of the Southwide Pine Seed Source Study.

PAST RESEARCH

Rees and Brown (8) report results of a 17-year-old red pine study in which the specific gravity of only one of 19 seed sources tested was significantly higher than all others. Echols (1) found highly significant variation in wood density among 15 seed sources of 17-year-old Scotch pine planted in New Hampshire, but he found no consistent trends associated with physiography or climate of provenances. Five-year-old loblolly from six seed sources examined by Thor and Brown (11) showed the wood density of one seed source to be significantly lower than three other sources. In 1967, Thor (10) re-examined the six seed sources after 10 years' growth and still found a significant difference in specific gravity between seed sources. He stated that the geographical trends did not follow those demonstrated for natural populations. Saucier and Taras (9) compared wood density among six seed sources of 8-year-old longleaf pine planted in Virginia. They found that one seed source (Florida) was significantly lower in wood density than all others, but evidence of frost damage in the plantation suggested that this difference in specific gravity was possibly associated with the lack of frost resistance in the Florida stock. A small but significant variation in wood density was reported by Goddard and Cole (5) in 5-year-old loblolly pine plantings that contained 18 seed sources from Georgia, South Carolina, and Florida. Gilmore et al. (2) showed no significant differences between seven loblolly pine seed sources grown in southern Illinois. They concluded that geographic race has little relation to specific gravity.

Jackson and Strickland (6) reported results of a 22-year-old loblolly pine planting in Georgia that contained 10 seed sources. They found wood density significantly correlated with longitude and latitude of seed source origins. Wood density increased westward with longitude from South Carolina to Texas, and northward with latitude from Georgia and Alabama to Maryland. These geographic trends are the opposite of those found for natural stands by Zobel and McElwee (14) and Wheeler and Mitchell (13). It appears, from the variation in results now on record, that additional seed source studies of wood density are needed to clarify this situation.

MATERIALS AND METHODS

The samples for this study were obtained from a planting of the Southwide Pine Seed Source Study located in Talladega County, Alabama. The planting was established jointly by TVA and Kimberly Clark Corporation during the 1952-53 planting season, and it has been maintained and periodically measured by Kimberly Clark foresters since that time. Nine seed sources were planted in a randomized, complete-block design with four replications. Each replication consists of 9 squares, each with 72 trees in border rows and 49 interior trees. Spacing is 6 x 6 feet. The seed sources represented in this planting are shown in figure 1 and listed below:

Alabama - Cullman County
Alabama - Jefferson County

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Arkansas - Clark County
Georgia - Wilcox and Crisp Counties
Louisiana - Livingston Parish
Maryland - Somerset County
North Carolina - Pamlico County
North Carolina - Onslow County
Texas - Angelina County

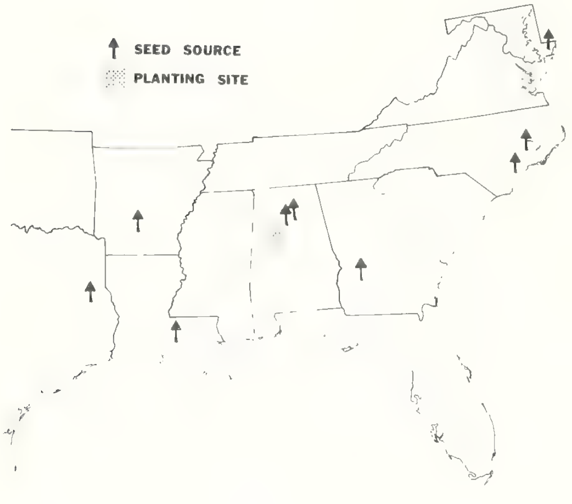

Figure 1.-Location of seed sources and planting site.

Prior to the loss of two replications of this planting in late 1965 from a marble-quarrying operation, 10 trees were randomly selected from all plots for a total study sample of 360 trees. The sample trees were cut down and a single disc, 3 inches thick, was removed from each tree at a point 5.3 feet above the ground. The d.b.h. and total height measurements were also obtained. The field collection was carried out by personnel from the Institute of Forest Genetics in Gulfport. These samples were shipped to the Southeastern Forest Experiment Station, Forestry Sciences Laboratory, Athens, Georgia, for analysis. At the time samples were collected, the planting was in its thirteenth growing season (14 years from seed).

Percent summerwood and ring width measurements were made across two opposing radii of the sample discs. The radii were chosen, after excluding areas containing compression wood, by randomly selecting a transect that passed through the pith. Measurements were made to the nearest 0.001 mm on a traversing dual-linear micrometer microscope.

Specific gravity was measured on two 45 degree wedges cut from each sample tree disc. Compression wood and knots were avoided when selecting the wedge-shaped samples. Green volume was determined by the water displacement method and the ovendry weight was determined by drying to a constant weight at 105° C. Specific gravity was determined on unextracted material only.

RESULTS

The average d.b.h., total height, annual rings in cross section, and specific gravity of the sample trees are presented in table 1. The most northern seed source (Maryland) had the highest average specific gravity of 0.435, while the Georgia seed source was lowest with 0.393. Excluding these high and low values, there was only a difference of 0.02 units in specific gravity separating the remaining seven seed sources. Analysis of variance for specific gravity (table 2) indicated a highly significant difference among seed sources, but a Duncan's multiple range test showed that the significant seed source difference was confined to the extreme values. That is, the Maryland seed source was significantly greater than only the Georgia seed source at the 5 percent level. The percent summerwood varied essentially in the same manner as specific gravity. The Maryland seed source had the greatest percent summerwood with 32 percent, and the Georgia seed source had the lowest with 22 percent. All other seed sources varied between 31 and 28 percent. Analysis of vari-

Table 1.--Average d.b.h., height, annual rings, percent summerwood, and specific gravity

Seed Source	D. B. H.	Hgt.	Rings in cross Sec.	Summer-wood	Specific Gravity [1]
	Inches	Feet	No.	Percent	Wt./vol.
Somerset Co., Md.	4.52	39.1	9.7	32	0.435
Onslow Co., N.C.	4.49	41.9	9.5	28	.426
Clark Co., Ark.	4.72	36.8	9.6	31	.424
Angelina Co., Texas	4.00	35.4	10.2	28	.422
Pamlico Co., N. C.	4.76	40.9	10.0	30	.417
Livingston Par., La.	4.54	40.9	10.2	31	.414
Jefferson Co., Ala.[2]	4.37	38.2	9.6	30	.412
Cullman Co., Ala.	4.46	37.1	10.1	28	.406
Wilcox & Crisp Co., Ga.	4.85	39.0	10.2	22	.393

[1] Green volume on ovendry weight basis.

[2] C-319, Local seed source.

Table 2.-Mean squares and test of significance for the analysis of variance of specific gravity and percent summerwood.

Source	d.f.	Specific gravity Mean squares	Percent summerwood Mean squares
Seed sources	8	0.005114**	0.027434
Replications	3	0.000996	0.013635
Experimental error	24	0.001093**	0.013972**
Sampling error	311	0.000370	0.004633

**Significant at 1 percent confidence level.

ance (table 2) for percent summerwood indicated a significant difference among seed sources at the 10 percent confidence level only. The experimental error for both specific gravity and percent summerwood was highly significant, indicating large individual differences among trees within plots.

Since gross wood yield is of primary importance for many uses, dry weight yields of seed sources were compared. These data are presented in table 3, which lists seed sources ranked from high to low in mean specific gravity, tree volume, and tree dry weight.

Tree volumes were calculated by using the conical formula $0.001818D^2H$ where D = diameter inside bark of sample discs and H = total tree height. Dry weight per tree was computed as follows:

Dry weight, lbs. = 62.4 x specific gravity x tree volume cu. ft.

Table 3 shows considerable shifting of seed source ranks when specific gravity and tree volume are compared. The Maryland seed source, which ranked first in specific gravity, ranked seventh in tree volume, while Georgia, which ranked last in specific gravity, ranked first in tree volume. There was an overall tendency for seed sources which ranked high in specific gravity to rank lower in tree volume and vice versa. The rank of seed sources by tree dry weight changed slightly from that of tree volume. The east North Carolina source ranked fifth in specific gravity, second in volume, and first in dry weight. Other seed sources changed rank order as they reflected the composite effects of specific gravity and tree volume. Table 4 shows correlations for tree and wood characteristics and several physiographic and climatic factors. The physiographic and climatic factors in these correlations are those found at the points of origin of the respective seed sources. In this group of relationships, specific gravity and percent summerwood were found to be significantly correlated at the 5 percent confidence level (r = 0.758*) as were tree volume and tree dry weight with June-August rainfall (r = 0.654* and r = 0.637*, respectively). The relationships between specific gravity and latitude, tree volume and longitude, and tree dry weight and longitude were not significant. In addition, specific gravity was negatively associated, but not significantly, with average annual temperature and January minimum temperature.

DISCUSSION

The nine seed sources in this planting had a

Table 3.--Comparison of mean specific gravity, volume, and dry weight

Specific gravity		Tree Volume[1]		Tree Dry Weight[2]	
Source	Wt/vol	Source	Cu. Ft.	Source	Pounds
Somerset Co., Md.	0.435	Wilcox & Crisp Co., Ga.	1.86	Pamlico Co., N. C.	47.36
Onslow Co., N. C.	.426	Pamlico Co., N. C.	1.82	Wilcox & Crisp Co., Ga.	45.61
Clark Co., Ark.	.424	Livingston Par., La.	1.69	Onslow Co., N. C.	43.86
Angelina Co., Texas	.422	Onslow Co., N. C.	1.65	Livingston Par., La.	43.66
Pamlico Co., N. C.	.417	Clark Co., Ark.	1.64	Somerset Co., Md.	43.43
Livingston Par., La.	.414	Cullman Co., Ala.	1.64	Clark Co., Ark.	43.39
Jefferson Co., Ala.[3]	.412	Somerset Co., Md.	1.60	Cullman Co., Ala.	41.55
Cullman Co., Ala.	.406	**Jefferson Co., Ala.**	1.40	**Jefferson Co., Ala.**	35.99
Wilcox & Crisp Co., Ga.	.393	Angelina Co., Texas	1.19	Angelina Co., Texas	31.33

[1] Volume in cubic feet = $0.001818D^2H$.

[2] Dry weight = 62.4 x specific gravity x volume.

[3] C-319, Local seed source.

Table 4.--Correlations among plot means for relationships between tree and wood traits and various physiographic and climatic factors at seed source origin.

Specific gravity x percent summerwood	.758*
Specific gravity x d.b.h.	-.336
Specific gravity x total height	.060
Specific gravity x latitude	.532
Specific gravity x longitude	-.235
Specific gravity x average annual temperature	-.496
Specific gravity x January minimum temperature	-.532
Specific gravity x annual precipitation	-.448
Specific gravity x June-August rainfall	-.150
Specific gravity x frost free season	-.144
Volume x latitude	.215
Volume x longitude	-.495
Volume x average annual temperature	.050
Volume x January minimum temperature	.105
Volume x annual precipitation	.193
Volume x June-August rainfall	.654*
Volume x frost free season	.125
Dry weight x latitude	.358
Dry weight x longitude	-.567
Dry weight x average annual temperature	-.082
Dry weight x January minimum temperature	-.033
Dry weight x annual precipitation	.097
Dry weight x June-August rainfall	.637*
Dry weight x frost free season	.006
Percent summerwood x latitude	.387
Percent summerwood x longitude	-.020
Percent summerwood x annual temperature	-.495
Percent summerwood x January minimum temperature	-.477
Percent summerwood x annual precipitation	.060
Percent summerwood x June-August rainfall	-.109
Percent summerwood x frost free season	-.160

*Significant at the 5 percent confidence level.

relatively narrow range of variation in specific gravity and percent summerwood after 14 years. Only two sources varied significantly from each other in specific gravity, and none in percent summerwood. Specific gravity and percent summerwood of the various seed sources tended to be associated with latitude, increasing from south to north (r = 0.532 and 0.387) but these were not significant. These trends are similar to those found by Jackson and Strickland (6) and others. On the other hand, volume tended to be associated with longitude, decreasing from east to west (r = -0.495). Tree dry weight reflects both specific gravity and tree volume, but this factor is more strongly associated with longitude, decreasing from east to west. The correlation of r = -0.567 was not significant.

These two weak trends, that is, specific gravity increasing from south to north, and volume from west to east, suggest that dry weight production should be highest from seed sources obtained in the eastern part of the species range. Such is the case since four of the first five seed sources in order of dry weight production are from this area.

Specific gravity did not vary with physiographic location of seed source origins but tree volume and tree dry weight did. The high values for dry weight were associated with coastal sources while the lower values were from inland sources. Wells and Wakeley (12), in their study of loblolly pine seed sources, showed similar growth responses; that is, trees from areas with wet summers and warm winters grew faster than those from areas with dry summers and cold winters. Areas with wet summer and moderate winter temperatures were mostly coastal. Of interest also was the significant correlation (r=0.654*) between tree volume and June-August rainfall. Trees from high rainfall seed sources tended to have greater volume growth, lower percent summerwood, and low specific gravity, but they are superior to other sources on a dry weight basis. Because these data are based on young material, it is likely that this correlation will change as percent summerwood increases with tree age.

SUMMARY AND CONCLUSIONS

In a 14-year-old planting of nine seed sources in Alabama, only the Maryland source had significantly higher specific gravity than one other source (Georgia). There was no significant difference in percent summerwood, wood volume, or dry weight.

There were no clear-cut trends in geographic variation, but specific gravity and percent summerwood tended to be associated with latitude, increasing from south to north, while volume and dry weight tended to be associated with longitude, decreasing from east to west.

High volume and, consequently, dry weight were associated with coastal seed sources, while the lower volumes were from inland sources. Trees from high rainfall sources tended to have greater volume growth, lower percent summerwood, and lower specific gravity, but they were superior to other sources on a dry weight basis. Performance of the local seed source was below average in all properties examined in this study.

Performance of coastal North Carolina seed sources was above average in all properties examined. The southwest Georgia seed source ranked first in volume and last in specific gravity, but in spite of its low specific gravity, it ranked second in wood dry weight.

It would be premature at this early plantation age to recommend non-local seed sources for this planting site. As evidence like this begins to accumulate, however, such practices may become advisable for some areas.

The genetic component of geographic variation in specific gravity does not appear to be large. If non-local seed are procured for the purpose of improving dry weight production, attention should be focused on those seed sources that exhibit above average tree characteristics of diameter, height, and taper.

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Variation in Photosynthesis and Respiration Among Loblolly Pine Progenies[1]

F. THOMAS LEDIG[2] and THOMAS O. PERRY[3]

Photosynthesis and respiration are of overwhelming importance to the production and accumulation of dry matter by plants. Unfortunately, the range of variability and the importance of the genetic control of these two aspects of metabolism, photosynthesis and respiration, has not been adequately measured in natural populations.

This report is based on a sample of families from the North Carolina State University and International Paper Company cooperative study of heritability in a natural population of loblolly pine (**Pinus taeda L.**) (Stonecypher, 1966). The objectives were to 1) determine whether variation in net and total photosynthesis, respiration, and P/R ratio exists within the population, 2) estimate components of variance and heritabilities for photosynthesis 3) estimate whether the major mode of inheritance of photosynthesis is of the additive or the dominance type, and 4) compare the rate of photosynthesis of the progeny of a cross between select trees from the North Carolina State University-Industry Tree Improvement Program with photosynthesis in the progeny of random crosses.

LITERATURE REVIEW

Though many estimates of heritability in forest trees are becoming available, little information pertinent to the estimation of genetic variance has been published on photosynthesis and respiration. With a total of 90 families from a stand of Douglas-fir, Campbell and Rediske (1966) measured photosynthesis and seedling dry-weight traits. They used a design 1 mating scheme in which each of a number of males is crossed to a different series of females. Their determinations extended over four months. Plants were held under a regime designed to keep them dormant. Dominance variance was found to be greater than additive variance.

Reines (1962) and Robertson and Reines (1965) investigated net photosynthesis and respiration in eight half-sib loblolly pine families and five half-sib slash pine families. Though they reported variation in photosynthesis among families the samples were small and heritabilities were not estimated. No variation in respiration was observed on a per unit weight basis.

Differences in photosynthesis were found between 16 poplar clones by Huber and Polster (1955), and the differences were related to variation in yield. However, variation in relative leaf area explained a greater proportion of the differences in yield than did photosynthetic rate. The poplar clones represented species and their hybrids and therefore this study does not indicate the degree of genetic variation found in natural populations.

MATERIAL AND METHODS

Material. Three experiments are reported which compare the photosynthetic and respiration rates of a sample of seedling progenies from crosses within a population of loblolly pine from southern Georgia. Two sets of trials were made with full-sib mating schemes and one with design 1. For the first full-sib trial, seed was germinated and seedlings were grown in pots under an open-sided polyethylene shelter until measurement in early October. For the second full-sib and the design 1 experiments, seedlings were placed in a greenhouse in mid-October and a supplemental photo-period was provided; measurements were made in mid-November.

Conditions of Measurement. Using a Beckman infrared gas analyzer, photosynthesis was measured as rate of CO_2 assimilation in a closed system with a flow rate of 750 cc. per minute. After the photosynthetic determination, the plant was covered with a dark-cloth and respiration measured as rate of CO_2 evolved in the dark.

Though it is desirable to measure photosynthesis under a variety of light intensities, temperatures,

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and seasons, this increases the difficulty of making a large number of comparisons among genotypes. Our experimental technique restricted the measurement to a maximum of two plants per hour. In addition, preliminary experiments indicated that replicates which extend over more than one day have high error due to large day-to-day variation. Because of these restrictions, comparisons could not be made over a range of light and temperature and conditions were employed which were representative of the Southeast in summer. A light intensity of 3000 ft. candles had been shown by Bormann (1956) to be near light saturation for loblolly pine seedlings with juvenile needles, and a temperature of 27°C (80° F) is common in the summer and near optimum for loblolly pine.

After the gas exchange measurements, the seedlings were disected into needles, stems, and roots and weighed to the nearest milligram. The resultant data were used to express photosynthesis and respiration on a dry weight basis.

Expression of Results. Net photosynthesis and respiration in mg of CO_2/hr are transformations of the time taken to change the CO_2 concentration of a given volume of air from 320 ppm to 270 ppm by volume. For comparison of genotypes, these rates must be divided by some measure of the photosynthetic surface or mass and the respiring mass, respectively. A per seedling basis is unsatisfactory because variation in leaf area or mass is greater than variation in photosynthetic rate. With fascicled needles (Kozlowski and Schumacher, 1943; Smith, 1967) or the leaves of hardwoods (Kramer, 1937; Kramer and Kozlowski, 1960), it is not difficult to estimate surface area, thus providing a common base for photosynthetic rates. Due to the lack of analogy with simple geometric figures, it is difficult to estimate leaf area for juvenile needles of pine. In addition, efficiency (production per unit cost) in terms of chemical energy production is more closely related to the mass of material required to produce a unit input than its surface area. Therefore, net photosynthesis was based on mg needle, and respiration on mg shoot, shoot being the dry weight of needles plus stem. The P/R ratio, cited as an efficiency index (e. g. Huber, 1964; Bordeau, 1958), is net photosynthesis in mg CO_2/hr divided by respiration in mg CO_2/hr.

Total photosynthesis was calculated as net photosynthesis plus respiration, both in mg CO_2/hr, divided by mg needles. The assumption involved in the estimation of total photosynthesis, i.e. that respiration in the dark equals that in the light, is probably incorrect. In many plants dark respiration is not the same as light respiration (e.g. Moss, 1966; Zelitch, 1958, 1965; Decker, 1955; Tregunna et al., 1961, 1964).

Experimental Design. All trials of photosynthetic and respiration measurements were randomized complete blocks with days as the block. In the first experiment, using progenies having full-sib relationships in the group, five replications and seventeen families were used. In the second set of trials, also with five replications, sixteen of the same families were compared. A combined analysis was performed, allowing measurement of genotype-environment interaction through the family times experiment component. The progeny of a cross between select trees of the North Carolina State University-Industry Tree Improvement Program was also included in each trial.

For the design 1 experiment, there were fourteen families consisting of seven male groups with two females in each, replicated six times. There were two replicates in each of three days. One of the male groups was represented by the progenies from controlled crosses between select trees.

FULL-SIB COMPARISONS

Components of variance attributable to differences among full-sibs may be interpreted as one-half the additive plus one-quarter of the dominance variance (Falconer, 1960). A heritability calculated on the basis of individual plants is considered a strict heritability. For full-sibs, the value lies between broad and narrow sense estimates. Narrow sense heritability is the ratio of the additive genetic variance to the total variance, so estimates based on the variance attributable to differences among full-sib families are upper limits of narrow sense heritability.

To interpret the families component of variation as one-half of the additive genetic variance for a trait plus one-quarter of the dominance variance requires the following familiar assumptions: 1) regular diploid and Mendelian inheritance, 2) population in linkage equilibrium, 3) relatives random members of a non-inbred population, 4) parents mated at random to produce progeny, 5) no epistasis, and 6) no maternal effects. Stonecypher (1966) discussed these assumptions for this population. Those assumptions concerning the relationships of members of progenies and parents might offer the most trouble in a natural stand where the degree of inbreeding and relatedness of individuals is unknown.

For the present investigation the assumption of no maternal effect deserves additional consideration. Correns in 1909 gave the now classic example of maternal effect in connection with cytoplasmic inheritance and his illustration may be directly applicable here. He found that the color of F_1 progeny of **Mirabilis jalopa** crosses was due to differences in chloroplasts and depended only on the phenotype of the female parent. In most plants the chloroplast is contributed to the embryo (probably in the form of proplastids) mainly through the maternal gamete. In **Pinus**, the cytoplasmic material carried by the pollen, including mitochondria and proplastids, disintegrates after segregating in one region of the fertilized oosphere and does not contribute to the embryo (Jinks, 1964). The light reaction in photosynthesis is localized in the chloroplast and therefore, differences in photosynthetic rate might be due to a genetically unalterable organization of the plastid. The result of differences in chloroplast structure would be variation attributable to maternal effect.

Results and Discussion

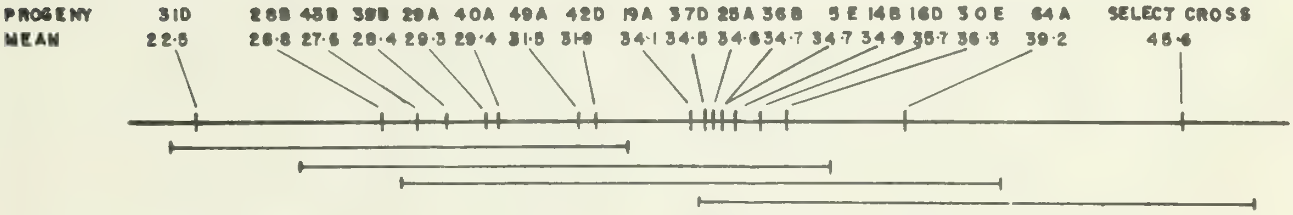
Full-Sib Experiment 1. The progeny of the select tree cross was superior in photosynthetic rate to the other progenies (table 1, Duncan's test). It had a rate of total photosynthesis of 51.8 mg CO_2/hr/mg needle which was 6.4 mg CO_2/hr/mg needle, or one-third of the entire range, above the progeny with the next highest rate of photosynthesis. Such a difference could account for a large divergence in growth between select seedlings and control seedlings in a matter of months if other factors contributing to dry matter production were equal. A t-test was valid in this case and indicated that the photosynthetic rate of the select tree progeny is significantly greater than that of the other families. Since the select tree progeny is a cross between wide geographic races, the observed superiority may be a result of hybrid vigor rather than selection.

This comparison of a select tree progeny with those from natural stands is the only one reported which can be interpreted on the basis of photosynthesis per unit needle weight. Wyatt and Beers (1964) compared the CO_2 assimilation of select tree progeny to control progeny over two years, using a nullpoint compensating system monitored by a gas chromatograph. Their results could only be applied on a per-seedling basis. Though it was true that their plus trees had a high capacity to assimilate CO_2, it was equally obvious that the plus trees were larger and had more leaf mass than the control seedlings.

The results of the analyses of variance (table 2) supply information on the quantitative inheritance of photosynthetic and respiration rates and seedling dry weight. While family differences in net and total photosynthesis and total dry weight were obvious, there are apparently no differences in respiration rate or P/R ratio. The difference among days of replication was important for all gas exchange measurements.

The genetic coefficients of variation for photosynthesis and for total dry weight are 0.09 and 0.22 respectively. Heritabilities are 0.28 and 0.34 for net and total photosynthesis, and 0.86 for total dry weight. The estimates indicate a fair amount of genetic variation in photosynthesis with much more variation in seedling dry weight. For photosynthesis, standard errors of the family components of variation are greater than half the size of the component and for total

TABLE I · DUNCAN'S NEW MULTIPLE RANGE TEST OF NET PHOTOSYNTHESIS IN μG CO_2/HR/MG NEEDLE FOR FULL-SIB EXPERIMENT NO·1



MEANS UNDERSCORED BY THE SAME LINE ARE NOT SIGNIFICANTLY DIFFERENT ON THE 5 PERCENT LEVEL OF PROBABILITY

Table 2. Mean squares and F-ratios for analyses of variance of net and total photosynthesis, respiration, P/R ratio, and total dry weight for full-sib experiment no. 1

		Net Photosynthesis		Total Photosynthesis		Respiration		P/R Ratio		Total Dry Weight	
Source	d.f.	mean square	F	mean square	F	mean square	F	mean square	F	mean square	F
Days	4	876.4791	17.81***	1061.6123	20.27***	8.6255	7.38***	14.6130	6.42***	25,571.6	3.13***
Families	16	90.0794	1.84**	106.8242	2.04**	1.2911	1.10 ns	1.6912	0.743 ns	39,089.8	4.78***
Residual	64	49.2022		52.3752		1.1695		2.2771		8,170.1	

ns non-significant

** significant on the 0.05 level

*** significant on the 0.01 level

dry weight they are less than half the component.

Phenotypic correlations of –0.288 (5% level) were found for both net and for total photosynthesis on total dry weight. However, **a priori** reasoning suggests that seedlings with higher photosynthetic rates should accumulate more rather than less dry matter. Negative correlations of photosynthesis and plant size may be due to 1) greater mutual shading of the needles in larger seedlings (Kramer and Clark, 1947) or 2) a decline in needle efficiency during the development of the seedling (Clark, 1961).

Zobel (1965) found strong negative correlations between apparent photosynthesis per dm^2 leaf surface on the one hand and leaf area per seedling on the other in sweetgum (**Liquidambar styraciflua L.**). Such a situation not only confuses any possible tendency of high photosynthetic rates to result in larger seedlings but may actually result in decreasing the rate of divergence in growth between seedlings with high and low photosynthetic rates respectively.

Full-Sib Experiment 2. There were many noticeable differences between Experiment 1 in which seedlings were conditioned out-of-doors and Experiment 2 in which pre-conditioning occurred in a greenhouse. Though net and total photosynthesis again varied among families, there were also differences in P/R ratio (table 3). This can be explained by the partial dependence of the ratio on photosynthetic rates which

Table 3. Mean squares and F-ratios for analyses of variance of net and total photosynthesis, respiration, P/R ratio, and total dry weight for full-sib experiment no. 2

		Net Photosynthesis		Total Photosynthesis		Respiration		P/R Ratio		Total Dry Weight	
Source	d.f.	mean square	F	mean square	F	mean square	F	mean square	F	mean square	F
Days	4	23.1834	2.83**	26.6452	2.96**	0.4237	1.96 ns	5.6230	2.75**	145,879.8	1.04 ns
Families	15	21.4780	2.62***	23.2112	2.58***	0.3616	1.67*	4.0806	1.99**	735,953.3	5.25***
Residual	60	8.1875		9.0094		0.2162		2.0484		140,260.5	

ns non-significant

* significant on the 0.10 level

** significant on the 0.05 level

*** significant on the 0.01 level

varied greatly.

Average photosynthetic rate was only two-thirds of that in the preceding experiment. Bormann (1956, 1958) has shown that loblolly pine seedlings having only juvenile needles, photosynthesize at a more rapid rate than seedlings with fascicled needles (presumably due to more self-shading in the latter).

The effect he observed was especially pronounced at the light intensity used in this study. Seedlings in Experiment 2 had mainly fascicled needles while those in Experiment 1 were almost entirely juvenile, perhaps accounting for the decrease in photosynthesis in the second experiment.

The progeny of the select tree cross had an average rate of photosynthesis. Racial variation makes the comparison between the select trees and those from the natural population inappropriate in this case. The parents of the cross between select trees were from the North Carolina piedmont and southwestern South Carolina provenances. The progeny were observed to be in a different physiological state than the southern Georgia material at the time of measurement and did not respond as vigorously to the conditions in the greenhouse. The reaction of piedmont loblolly is typical of northern races.

Heritabilities for net and total photosynthesis were 0.50 and 0.48, respectively. The relative increase in precision and apparent increase in heritability between this and the preceding experiment is due to a great decrease in total variation and in particular to the error variance. Probably the buffering of the environment by the controlled temperature and photoperiod in the greenhouse is responsible for reducing the variation. Variation among days in photosynthesis and respiration was obvious, however.

Phenotypic correlations between both net and total photosynthesis on the one hand and total dry weight on the other were not statistically significant.

Combined Analysis. The results of the combined analysis using the 16 families common to both experiments are summarized in terms of components of variance and heritabilities in table 4 along with the statistics for each experiment separately. In the combined analysis, the families component of variance is small and heritabilities for net and total photosynthesis are 0.07 and 0.08.

Table 4. Estimates of means, variance components, standard error of the genetic component, genetic coefficient of variation, and heritability for net and total photosynthesis and total dry weight for each experiment separately and for both experiments combined.

PARAMETER[a]	NET PHOTOSYNTHESIS (μgm CO_2/hr/mgm needle)			TOTAL PHOTOSYNTHESIS (μgm CO_2/hr/mgm needle)			TOTAL DRY WEIGHT (mgm)		
ESTIMATED	Expt. no. 1	Expt. no. 2	Combined	Expt. no. 1	Expt. no. 2	Combined	Expt. no. 1	Expt. no. 2	Combined
μ	32.87	23.61	27.97	38.81	27.15	32.72	362	1645	990
$\sigma^2 e$	49.202	8.188	29.986	52.375	9.009	32.324	8,170	140,260	74,254
$\sigma^2 gxe$	—	—	4.272	—	—	5.461	—	—	54,410
$\sigma^2 g$	8.175	2.658	1.213	10.890	2.840	1.398	6,184	119,139	8,230
$\sigma_{(\sigma^2 g)}$	6.245	1.502	5.653	7.351	1.625	6,551	2,621	50,737	37,846
$\sigma g/\mu$	0.09	0.07	0.04	0.09	0.06	0.04	0.22	0.21	0.09
h^2	0.28	0.50	0.07	0.34	0.48	0.08	0.86	0.92	0.11

[a] μ

σe^2 = variance due to random error

$\sigma^2 gxe$ = variance due to the interaction of families in experiments

$\sigma^2 g$ = variance due to differences among families

$\sigma_{(\sigma^2 g)}$ = standard error of estimate of the component of variance due to differences among families

$\sigma g/\mu$ = genetic coefficient of variation

h^2 = heritability computed as $2\sigma_g^2 / (\sigma_e^2 + \sigma_g^2)$ for each experiment and $2\sigma_g^2/(\sigma_e^2 + \sigma_{gxe}^2 + \sigma_g^2)$ for both experiments combined

This reflects the relatively large interaction component between families and experiment, i.e. between families and the conditions under which they were grown and the time of measurement. There is no other data in the literature on the magnitude of genotype-environment interactions of photosynthetic rate on the population level. The present experiment does not identify the source of the interactions found but suggests that they are of overriding importance. It is likely that the genes functioning under one set of conditions may not be the same as those operating under other circumstances.

As a manifestation of the interaction there was almost no correlation between the performance of progenies in the two trials. It is interesting to speculate on the outcome of Campbell and Rediske's (1966) experiment repeated when the seedlings are not held dormant. The knowledge provided by this study indicates that there may be little relationship between the ranks of progenies in photosynthesis under different preconditioning. The estimates of heritability obtained by these authors, 0.21 and 0.53 based respectively on a variance attributable to all plots and a variance within plots, are close to those reported here.

The difficulty in investigating photosynthesis and respiration as genetic traits occurs because both traits are far from gene action. The manifold effects of the environment in modifying photosynthesis suggests that feedback from many interacting metabolic pathways is involved. Gas exchange, i.e. uptake of CO_2 in the light for net photosynthesis and release of CO_2 in the dark for respiration, is an end result of the processes of the entire metabolic system. Still, if yield is a suitable trait for breeders, then photosynthesis may also be, for the observed dry weight of a plant almost entirely represents the balance in organic carbon between CO_2 assimilated and that respired again as CO_2. However, it is presumptuous to expect that measurement of photosynthesis and respiration under one set of conditions can be related to the summation of these processes, the final plant weight.

DESIGN 1 EXPERIMENT

Design 1, developed by Comstock and Robinson (1948, 1952) can be used to divide genetic variation into additive and dominance components. This design mates each of a series of male parents to a different sample of female parents. Half-sib components are estimated from the males mean square and represent one-quarter of the additive variance and none of the dominance. The females-in-males component is a measure of the variance among full-sib families minus the variance among half-sibs and estimates one-quarter of the additive plus one-quarter of the dominance variance. Therefore, any difference between the males and the females component should indicate the presence of dominance deviation. The assumptions discussed above for the full-sib case apply to the estimation of components from the females-in-males mean square in this experiment.

Results and Discussion

In the experiment using design 1 the female-in-male mean square is larger than that of the males for both net and total photosynthesis (table 5). The relative importance of the female-in-male source of

TABLE 5.--Mean squares and F-ratios for analyses of variance of net and total photosynthesis, respiration, and P/R ratio for a design 1 experiment

		Net Photosynthesis		Total Photosynthesis		Respiration		P/R Ratio	
Source	d.f.	mean square	F	mean square	F	mean square	F	mean square	F
Days	2	71.2248	2.106 ns	52.7783	1.571 ns	9.3523	10.106 ***^{a}	83.1520	5.064 ***^{a}
Reps/Days	3	33.8138	3.143 ***	33.5983	2.496 *	0.4560	0.481 ns	0.7229	0.128 ns
Males	6	31.8920	0.294 ns	44.1359	0.339 ns	1.0808	0.592 ns	1.0709	0.102 ns
Females/Males	7	108.4409	10.079 ***	130.1963	9.671 ***	1.8246	1.926 *	10.4693	1.851 *
Residual	65	10.7587		13.4623		0.9474		5.6564	

ns non-significant
ns non-significant
* significant on the 0.10 level
** Significant on the 0.05 level
*** significant on the 0.01 level
a based on the pooled mean square of times-days plus residual

variation compared to the male source suggests that much of the genetic variation in photosynthetic rate may be of the dominance or dominance-epistatic types predominantly. However, a smaller and inadequate preliminary experiment had indicated that all variation was associated with the males or additive component. (Ledig, 1967). Dominance variation for net photosynthesis was 1.7 times greater than additive genetic variance in the study of Campbell and Rediske (1966) on seedling Douglas-fir. Thus there may be some significance to the results of the present experiment which indicate a high female-in-male component. The relative importance of maternal effect has not been assessed, however, and designs using reciprocal crosses are necessary to clarify this situation. The use of paternal half-sib families would permit estimation of genetic constants by avoiding the problem of maternal effect but the production of large numbers of paternal half-sib progenies is not practical with forest trees.

SUMMARY AND CONCLUSIONS

For net photosynthesis, the two estimates of heritability, 0.28 and 0.50, based on individuals from full-sib families are of moderate size. These must be considered somewhat larger than narrow-sense heritabilities since besides the additive variance they presumably contain half the dominance variance. They are the only estimates available of heritability for photosynthetic rate in loblolly pine.

From the combined analysis of these two experiments, it was obvious that a progeny's performance when grown under one set of conditions may have no correlation with its performance when grown under other environments. Genotype-environment interaction seems to be of overriding importance, and day to day variation is also an important variable in photosynthetic measurements. Photosynthesis, as measured by gas exchange, in seedlings preconditioned by one environment may not be the same process as that measured when preconditioning occurs under other environments. Likewise, photosynthesis under one set of light, temperature, and moisture conditions may not be the same trait as photosynthesis under a different set of measurement conditions because the functioning genes may be different.

Because of the many environmental effects on photosynthesis and the inability to ascribe variation in gas exchange to one process, overly-simplified genetic experiments will be unprofitable. Studies which determine the reaction of the genotype to the range of environmental modifiers of photosynthetic rate are required.

Design 1 experiments of the size reported are too small for estimation of variance components. However, this experiment suggests that genetic variation in photosynthesis may be predominantly of the dominance or dominance-epistatic types. At least one other explanation of these results exists: maternal effect. High female components may indicate that in addition to dominance variance there are differences in chloroplasts which are apparently inherited entirely through the seed parent in **Pinus**. Designs utilizing reciprocal crosses are recommended to clarify the significance of high "dominance" variance.

When progeny of a cross between select trees was compared near the seasonal peak of photosynthesis to progenies from random matings, the select tree progeny was greatly superior in photosynthesis in μg CO_2/hr/mg needle. This is the first time such a comparison has been reported and may indicate that the intensive selection practices of the cooperative Tree Improvement Program have resulted in selection of photosynthetically superior trees. The alternative hypothesis is that the progeny of the select tree cross exhibited hybrid vigor because it is a wide cross between geographic areas.

No correlation, or very weak negative correlations, were seen between photosynthetic rate and seedling dry weight in this investigation. Because the rank of progenies in photosynthetic rate may change with environmental variation, prediction of dry matter production can only be made by integration of the photosynthetic response over the diurnal and seasonal cycles, eliminating the possibilities of making selections by a simple method. Model systems and growth chambers are required. Such an approach to the problem has begun.

Decker (cited by Campbell and Rediske, 1966), Kramer (1958), and Bourdeau (1958) have all suggested the possibility of using the infra-red gas analyzer to select trees. This approach may still have merit. However, the high sampling error from branch to branch when photosynthesis is measured on excised or attached twigs would seem to preclude such selection as a practical method among mature trees. Measuring photosynthesis in second year shoots from grafted ramets may offer attractive possibilities for the early testing of clones in grafted seed production orchards.

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Inheritance of Spiral Grain in Young Loblolly Pine [1]

BRUCE J. ZOBEL, ROY W. STONECYPHER, AND CICELY BROWNE [2]

Summary

A study of spiral grain on material from 52 control-pollinated families of four-year-old loblolly pine indicated that genetic variation in this trait is of the nonadditive type. This study involving 1043 trees suggests that mass selection to reduce spiral grain will not be very effective in loblolly pine if the pattern for older trees is similar to the young trees studied. The trees were only four years of age but spirality was measured in that portion of the tree where it often attains maximum values. Only rarely was a tree found with spirality bad enough to cause serious degrade in sawn or veneer products. The study raises some question whether spiral grain in loblolly pine is either widespread or serious. The reference or datum from which degree of spirality is determined is important; since spirality was measured as deviation from pith, results must be interpreted in this light.

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[1] The text of this paper will be printed in the proceedings of the International Union of Forest Research Organizations meeting in Munich 1967. The work was conducted at Southlands Experiment Forest, Bainbridge, Georgia with cooperation of North Carolina State University, National Science Foundation, and National Institute of Health.

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The Effect of MH30 on Grass and Pines

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The Beech Creek Seed Orchard near Murphy, N. C., presently covers 240 acres. It is in an area of rolling land with 5 to 30 percent slopes. Because of the topography it was necessary to establish a heavy grass cover. Problems of shading and crowding of ramets developed. In addition the tall grass made it difficult to see the smaller ramets and stakes, therefore some were lost when mechanical equipment was used in the orchard work. Mechanical equipment and some hand labor was tried to reduce the grass cover around the ramets, but these operations proved quite expensive. What was needed was a method to reduce the cost.

In addition it was felt that a method was needed to reduce the height of the ramets, without reducing the production of viable seed. If this could be done, there would be considerable savings in the cost of orchard treatments, such as spraying for insects and diseases, cone collection, mowing, etc.

With these problems in mind I contacted U. S. Rubber to get any information they might have available on the effectiveness of maleic hydrazide (MH30) as a growth retardant

MH30 had been used for over eight years as a growth retardant of grass. (1) There was a wide range of results from the different tests on grasses. They ranged from no control through the killing of the grass. A majority of the tests, however, showed some degree of height control.

In some of the tests with conifers, Trandeen, (2) obtained a shortening of internodes and distance between whorls of Christmas trees: Rai and Hamner, (3) found that growth of scotch and jack pine was inhibited two weeks after spraying but effects were less pronounced at the end of the summer.

From this information it was decided to set up an operational area for grass height control. An acre of fairly level bottomland site was selected. It was covered with a heavy stand of Kentucky 31 fescue except for small patches of white dutch clover and a small patch of sedge grasses. The area was treated with a spray mix of: 4 pounds acid equivalent of MH30 in 50 gallons of water. The mixture was applied, using 3-gallon pressure type hand sprayers. The spraying was done the last of May, and at a time when no rain was forecasted for over twenty-four hours. This gave favorable conditions for the absorption of the MH30 by the grass. Because MH30 is soluble in water, rain will reduce the effectiveness of the chemical by washing it off the plants. A check was made in July to see what effect the MH30 had on the treated area. The treated grass averaged about 18 inches tall; the untreated was over 36 inches tall. The treated grass had very few seed heads while the untreated grass had a heavy seed crop. In addition the treated grass had heavier and thicker leaves. This was probably due to the action of MH30 which inhibits cell division, but will allow cell growth.

The MH30 appeared to have no effect on either the clover or the sedge grasses.

In April 1966 an application of MH30 was made along the unplanted stake rows for grass height control. The mixture was applied at the same rate as had been used previously, in a band about three feet wide along each row. A trailer mounted Berkly pump, developing 35 PSI, was used to spray the area. No attempt was made to saturate the area.

Some of the sprayed area was planted with shortleaf, Virginia and white pine ramets in June and July. There were no visible effects on these trees. Hoffman, et al. (4) found that plants took up very little maleic hydrazide from the soil under a normal spray program.

As on the previously treated area the treated grass was shorter and had very few seed heads. The treated areas also had a darker green appearance than the untreated areas. The reduction in the number of seed heads helped reduce the amount of new grass coming in around the ramets during the latter part of the summer. This will be of considerable help this year as we plan to reduce the depth of our mulch due to our rodent problem.

In July, I sprayed some Virginia pine and white pine seedlings with a mixture of 4 pounds acid equivalent MH30 in 50 gallons of water. The spray was applied to the drip point. Two weeks later a check was made to see what, if any, the effects were. There appeared to be no effect on the white pine but the branch tips on the Virginia pine were

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killed back for three or four inches.

A check this spring showed some of the Virginia pine were beginning to produce new shoots but the recovery was erratic. The spring check of the white pine showed some killing of the branch tips with no apparent new growth. A check made the last of May showed some Virginia pine had been killed.

Two different methods of MH30 spray applications were made in May of this year. The first spray application was made directly to the shortleaf pine and white pine crowns. The second spray application was made to the grass around the base of the seedlings. No attempt was made to keep the spray from getting onto the seedlings. The mixture was the same (4 pounds acid equivalent in 50 gallons of water) as had been used previously.

After two weeks no effect has been observed.

Summary

Maleic hydrazide has given satisfactory results as a growth retardant for grass on the Beech Creek seed orchard. It not only reduces the heights of the grass but also reduces its ability to produce seed.

When used on pines in limited tests, MH30 killed back the branch tips on Virginia pine and white pine. Further testing is needed to find out if this chemical could be used effectively as a growth retardant in seed orchards.

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Racial Variation in Sand Pine Seedlings[1]

JOHN E. MORRIS[2]

Interest in sandhills reforestation has substantially increased the economic importance of sand pine (**P. clausa** (Engelm.) Sarg.). This species has demonstrated superior growth compared to longleaf (**P. palustris**, Mill.) and slash pines (**P. elliottii** Engelm.) on certain sandhills sites (Florida Forestry Reporter 1963). Its kraft pulp properties of overall strength and brightness compare favorably to those of longleaf pine (Martin 1962).

Sand pine is geographically confined to the excessively or moderately well drained and infertile sands of Florida and the southern tip of Baldwin County, Alabama (fig. 1). The major concentration is a 280,000 acre block in north central Florida. The only other extensive area is in western Florida, between Panama City and Pensacola.

Sand pines are typically small, poorly formed and short-lived. The average stand attains a height of about 65 feet and a maximum diameter of 18 inches. Stands usually deteriorate after 50 to 60 years (Cooper 1957). Sand pine is related genetically to Virginia pine (**P. virginiana** Mill.).

Two races of sand pine are recognized. The Ocala race has serotinous cones, grows in even-aged stands, and is phenotypically of poorer form than the open-coned and uneven-aged western race. Ward (1963) has named the western race **immuginata.**

Relatively little research has been conducted on sand pine. This increasingly important species may facilitate sandhills reforestation and should, therefore, be evaluated more thoroughly. The objective of this study was to investigate possible racial variation of certain seedling characteristics, especially growth rate and response to fertilization.

PROCEDURE:

In the fall of 1965, fresh cones were collected from eight average dominant trees in each of five Florida counties; Walton, Franklin, Levy, Marion and Hernando (fig. 1). At each location the randomly selected trees were within the same soil series and a minimum of 300 feet apart. The soil series at Franklin, Levy and Hernando counties was St. Lucie. The Marion and Walton County soils were better sites; Kershaw and Lakeland sands, respectively.

The seedlings were kept separate by individual mother-tree and grown five to a pot (one line from each origin) in a ventilated and shaded greenhouse for eight months. The Marion County Kershaw soil was treated with a factorial combination of 0 to 100 ppm of nitrogen and 0 to 300 ppm of phosphorus.

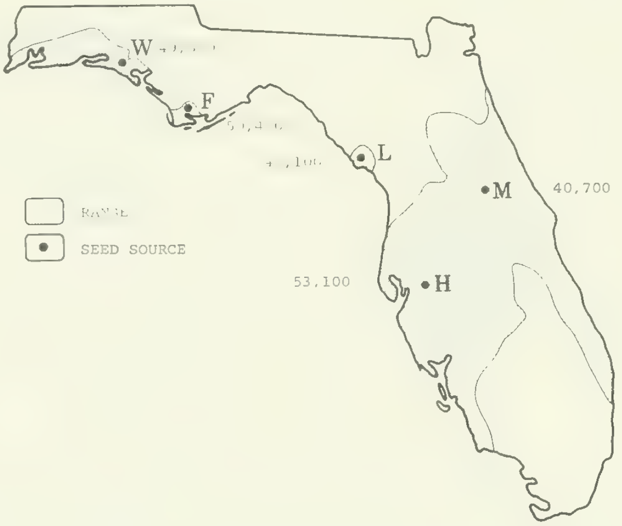

FIG. 1. RANGE, SEED SOURCE, AND SEED SIZE (SEEDS/LB.).

RESULTS AND DISCUSSION:

Seed Color and Seed Size: Seed color darkened and seed size increased from west to east (fig. 1). These trends were reported previously by Barnett and McLemore (1966) in a comparison of Walton and Franklin seeds. The small size of the Hernando seeds was an exception. Walton and Franklin seed were significantly smaller than Levy, Marion and Hernando seed and the Marion seed were significantly larger than the Levy and Hernando seed; Hernando seed were significantly smaller than Levy seeds (table 1).

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[1] Portion of a thesis to be submitted by the author in partial fulfillment of requirements for a Master Degree at University of Florida.

[2] Research Forester, Buckeye Cellulose Corporation, Perry Florida.

Table 1

Analysis of Variance

Variable	Source of Variation	df		Level of Significance
Cotyledon Number	Origins	4		
	W+F vs L+M+H		1	ns
	W vs F		1	ns
	M vs L+H		1	ns
	L vs H		1	ns
	Lines in Origins	35		**
Seed Size	Origins	4		
	W+F vs L+M+H		1	**
	W vs F		1	ns
	M vs L+H		1	**
	L vs H		1	**
	Lines in Origins	35		**
Seed Color	Origins	4		
	W+F vs L+M+H		1	**
	W vs F		1	ns
	M vs L+H		1	ns
	L vs H		1	ns
Deficiency Symptom (Yellow Tipping)	Origins	4		
	W+F vs L+M+H		1	**
	W vs F		1	ns
	M vs L+H		1	ns
	L vs H		1	ns

Cotyledon Number: No differences by seedling origin were observed in the number of cotyledons. The most frequent number of cotyledons was five. The range by individual seedlings was from three to seven. The range by lines was 4.30 to 5.70 and was statistically significant (table 1).

Deficiency Symptoms: Significant differences in deficiency symptoms occurred both by seedling origin and by treatment. The nitrogen alone treatment resulted in stunted growth and purplish needles, a typical phosphorus deficiency. This effect was uniform for all origins. Seedlings with yellow tips which later turned brown were present only in the NP treatment. These symptoms are similar to the magnesium deficiency symptoms of Virginia pine reported by Sucoff (1961). The Walton and Franklin seedlings exhibited such symptoms to a significantly less degree than did the Levy, Marion and Hernando seedlings (table 1).

Mycorrhizae: Ectotrophic mycorrhizae were completely absent in the presence of 100 ppm of nitrogen. However, the proportion[1] of infection was unaffected by 300 ppm of phosphorus. Walton and Franklin origins showed significantly more mycorrhizal infection than those from Levy, Marion, and Hernando (table 2).

Although the overall root infection of Walton seedlings was greater than that of Franklin seedlings the latter exceeded the Walton seedlings in proportion of infection in the phosphorus alone treatment.

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[1] Each seedling was subjectively evaluated for root infection and placed in the following categories--none, very low, low, medium, high.

TABLE 2
Analysis of Variance

Source of Variation	df		Mycorrhizal Infection Level of Significance	Shoot Weight Level of Significance
Fertilizer	3			
N		1	**	ns
P		1	ns	**
NP		1	ns	**
Origin	4			
a) W+F vs L+M+H		1	*	**
b) W vs F		1	ns	**
c) M vs L+H		1	ns	ns
d) H vs L		1	ns	*
Fertilizer x Origin	12			
N x a		1	ns	ns
N x b		1	ns	**
N x c		1	ns	ns
N x d		1	ns	ns
P x a		1	ns	**
P x b		1	*	**
P x c		1	ns	ns
P x d		1	ns	ns
NP x a		1	ns	ns
NP x b		1	ns	ns
NP x c		1	ns	ns
NP x d		1	ns	ns

The absence of mycorrhizae may have led to the deficiency symptoms mentioned above. The nitrogen alone treatment resulted in no mycorrhizal infection, and phosphorus deficiency symptoms were evident. These stunted and purplish seedlings fit the description of Virginia pine seedlings grown in the absence of mycorrhizae (McComb 1938). The nitrogen plus phosphorus treatment resulted in yellow tipping, a possible magnesium deficiency. These observations further substantiate the importance of mycorrhizae in absorption of nutrients.

It seems reasonable that in the absence of mycorrhizae, the most unavailable nutrient, phosphorus, would indicate a deficiency symptom first. Upon the addition of phosphorus, the next most unavailable nutrient, possibly magnesium, may indicate a deficiency symptom.

Shoot Weight: Shoot weights were significantly different by seedling origin, by fertilizer, and by the origin x fertilizer interaction (fig. 2, table 2). All shoot weights were severely decreased in the nitrogen alone treatment and mortality was high (15%). All shoot weights, with the exception of the Walton seedlings, were positively affected by the phosphorus alone treatment. Interestingly, it was found that all origins responded synergistically to the NP treatment (table 2). The nitrogen x the Walton and Franklin comparison was significant; the nitrogen main effect was positive for Franklin and negative for Walton shoots.

The interactions of nitrogen and phosphorus with the Walton and Franklin comparison are of considerable practical significance as this relationship reduces the importance of the main effects of the fertilizer. It follows that seed origin must be considered before response to fertilizer can be predicted with any degree of confidence.

In conclusion, for a geographically small species sand pine's regional variation is striking. Under the conditions of reproductive isolation and environmental differences, both ecotypic and clinal variations have developed. To capitalize effectively on the probable existence of racial variation of economically important traits, these races must be evaluated genetically in order to secure the most efficacious race for a given site and cultural regime.

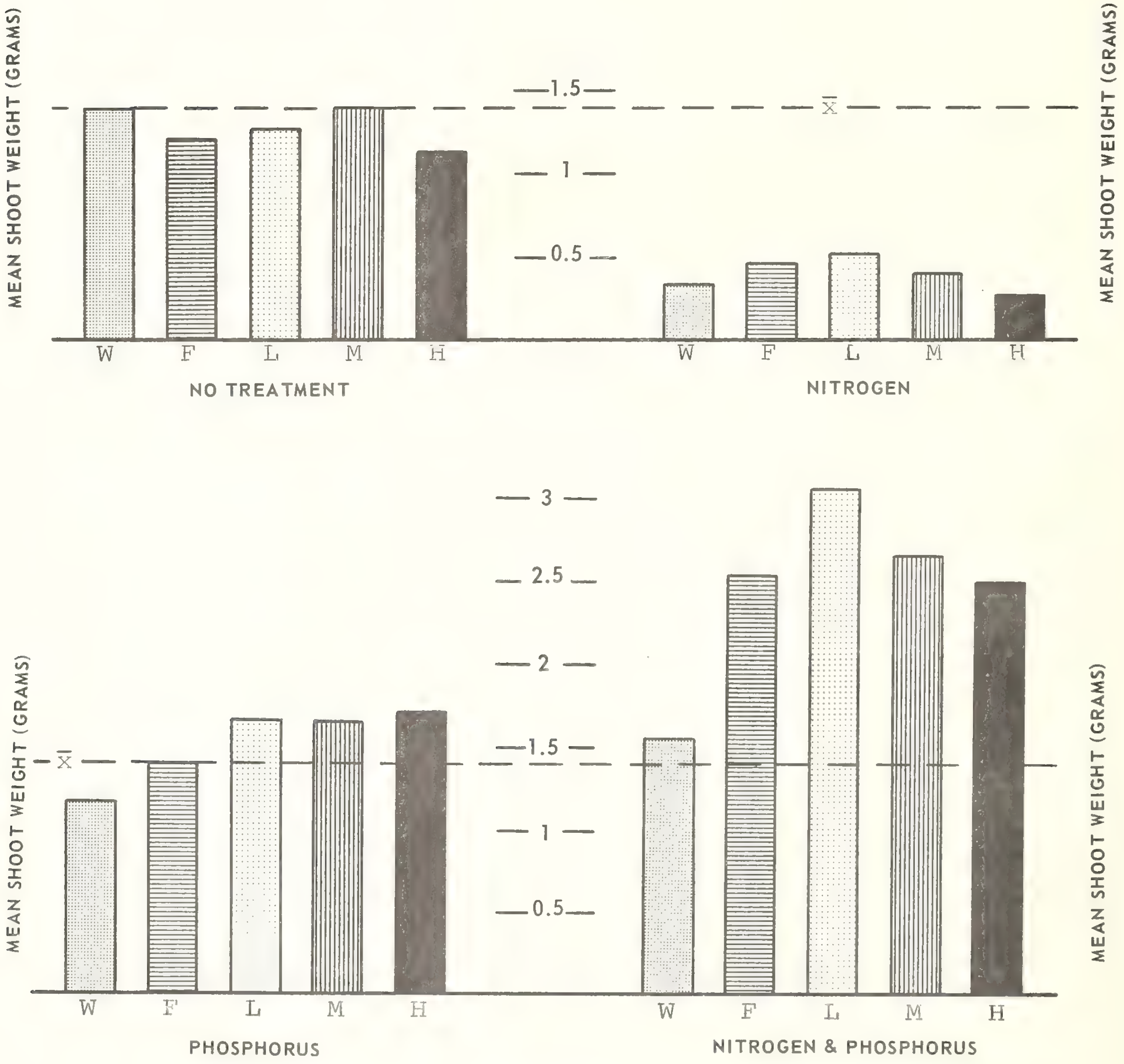

FIGURE 2. SHOOT WEIGHT BY SEED SOURCE AND FERTILIZER TREATMENTS

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